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OENOTHERA · LAMARCKIANA,
A Mutating Species.

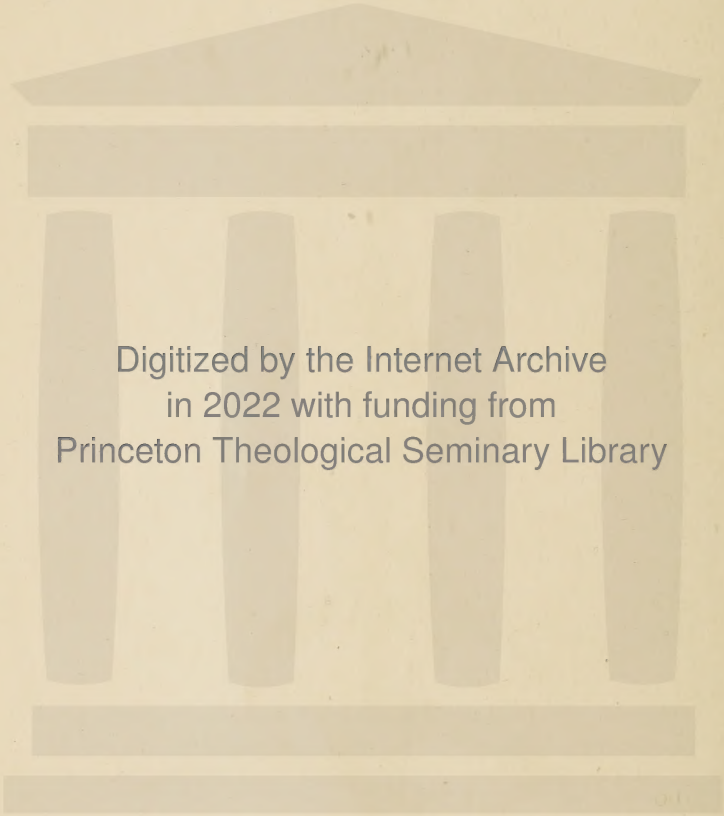
Martin, Hood & Larkin Lith. London, W.C.

OENOTHERA GIGAS,
Originated in 1895.

Martin Hood & Larkin, Lith. London, W.C.

OENOTHERA ALBIDA,
Produced Yearly by the Parent-Species.

Martin Hood & Larkin lith. London, W.C.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A MUTATION IN A FAMILY OF OENOTHERA LATA.
Origin of Oenothera albida.

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OENOTHERA SCINTILLANS.

OENOTHERA OBLONGA.

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THE MUTATION THEORY

EXPERIMENTS AND OBSERVATIONS
ON THE
ORIGIN OF SPECIES IN THE VEGETABLE KINGDOM

BY
HUGO DE VRIES
PROFESSOR OF BOTANY AT AMSTERDAM

TRANSLATED BY
PROF. J. B. FARMER AND A. D. DARBISHIRE

VOLUME I
THE ORIGIN OF SPECIES BY MUTATION

WITH NUMEROUS ILLUSTRATIONS AND FOUR COLORED PLATES

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1909

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AUTHOR'S PREFACE TO THE TRANSLATION.

The promulgation of the principle of unit-characters is the main theme of this work, as is emphasized in the first sentence of the Introduction. At the time of the publication of the first part of the German edition (1900) this principle was new and was also in evident opposition to the current belief in the slow and gradual evolution of the organic world. During the years that have since elapsed, it has gained almost universal acceptance, though there are still some authors, especially among zoologists, who are opposed to it.

The evidence which supported this view was derived from three main sources.

First a clearer understanding of the processes of selection in agricultural plant-breeding. This conception has since been corroborated in the most convincing manner by the work of NILSSON and of KORSCHINSKY, and it points to the elementary species as the real material for artificial and natural selection.

Secondly, the experimental evidence afforded by the evening primroses and some other groups of plants; especially the observed origin of *Oenothera gigas*, which appeared suddenly in my cultures in the year 1895 and possessed, at its first origin, all the attributes of a new species, including constancy and even a double number of chromosomes in its nuclei.

Thirdly, the new light, thrown by the principle of the unit-characters on the work of MENDEL, neglected up to

that time, which even FOCKE in his standard work on Plant-hybrids did not give the rank of a work of first-rate importance. The work of BATESON and of his school, of CUÉNOT, WEBBER and many others, but above all that of DAVENPORT, have since brought the principle of unit-characters to its now prominent rank in the study of hybridization.

There can be no doubt, that this principle of the unit-characters opens up a wide range of questions and subsidiary theories, which may now be subjected to experimental inquiry and critical study. The phenomena of inheritance and hybridization constitute a wide field, which had scarcely been explored hitherto. Half- and middle-races, with their apparently incomplete heredity, constant hybrids, correlated and associated characters, and many other most curious phenomena afford plenty of scope for future investigation.

Under these circumstances I feel deeply indebted to Professor FARMER and Mr. DARBISHIRE for their painstaking work in preparing an English translation of this book, as well as to Dr. PAUL CARUS of the Open Court Publishing Co. for his liberality and full confidence in the scientific and practical value of the principles enunciated therein. Great support has already been accorded to my ideas by many English and American workers in this field, and it is confidently hoped, that this translation will secure that universal cooperation without which no great scientific principle can attain its full measure of usefulness to mankind.

No essential changes have been made in the translation, with the exception of those which have been made necessary by the work of HJ. NILSSON on the selection and the improvement of cereals in Sweden. Corrections of minor points have been introduced wherever necessary.

It is proposed to publish this translation in two independent volumes, the first dealing with the origin of species by mutation, the second with the origin of varieties and with the general considerations found at the end of the

German edition. Some chapters, especially among those on hybridization, which seem to be of too technical a nature for the general student, will be omitted from the second volume. It is proposed to publish their translation in a separate work.

Amsterdam, June 1908.

Hugo de Vries.

TRANSLATORS' PREFACE.

The task of preparing this translation has been made lighter by the knowledge that the need for it is urgent. Professor De Vries's successful attempt to bring the process of specific differentiation within the sphere of experimental inquiry is now recognized as a landmark in the history of our knowledge of these phenomena. But those who take part in the discussion of evolutionary questions are rarely equipped with even a superficial familiarity with the broad features of Professor De Vries's investigations and ideas, and, still less, with (what should be a minimum qualification for a participant in such discussions) a detailed knowledge of the contents of *Die Mutationstheorie.*

It is hoped that this translation will help to remedy this state of affairs. This much, at any rate, is certain, that the evidence, collected by De Vries up to 1901, bearing on the question of the origin of species and varieties by mutation, is now for the first time available to the student of evolution who cannot read German.

In the translation itself we have endeavored to convey the author's meaning as faithfully as possible rather than to provide a word for word translation of the German. And to this end we have, wherever it seemed necessary, split sentences into two, or run two into one, or made other such additions and omissions as seemed desirable. All of these alterations have been examined and approved by the author.

We hope that our translation of this great work will help to bring us closer to an understanding of one of the most puzzling manifestations of vital activity—that of specific diversity.

J. B. Farmer.
A. D. Darbishire.

PREFACE TO THE FIRST VOLUME.

The origin of species has so far been the object of comparative study only. It is generally believed that this highly important phenomenon does not lend itself to direct observation, and, much less, to experimental investigation.

This belief has its root in the prevalent form of the conception of species and in the opinion that the species of animals and plants have originated by imperceptible gradations. These changes are indeed believed to be so slow that the life of a man is not long enough to enable him to witness the origin of a new form.

The object of the present book is to show that species arise by saltations and that the individual saltations are occurrences which can be observed like any other physiological process. Forms which arise by a single saltation are distinguishable from one another as sharply and in as many ways as most of the so-called small species and as many of the closely related species of the best systematists, including LINNAEUS himself.

In this way we may hope to realize the possibility of elucidating, by experiment, the laws to which the origin of new species conform. The results of these studies can then be compared with those which have been obtained with systematic, biological and particularly with palæontological data. A most remarkable agreement will be found to exist between these and my new results.

These saltations, or mutations, of which the so-called

sports are the best known instances, constitute a distinct province in the study of variability. They occur without transitional gradations and are rare; whilst ordinary variations are continuous and always present.

The whole subject of variability, therefore, falls into two sections, one of which includes the ever present, individual or fluctuating variability, whilst the other embraces mutability. The former phenomena conform to the well-known laws of probability and are determined by general nutritional conditions; they also afford the material for the production of many of the so-called improved races of agriculture.

Mutations give rise not only to species but also to varieties; and, as has been recognized for a long time, they play an all-important rôle in horticulture. An exhaustive comparative and experimental study of horticultural varieties is an indispensable preliminary to a complete treatment of the problem of the origin of new forms. It will be given in the second volume.

The generalizations here outlined apply obviously to animals as well as to plants. Though as a botanist I have confined my attention to the latter, I am convinced that my results will be confirmed in the realm of the animal kingdom. Again a proper distinction between variability and mutability is of the greatest importance from the point of view of the application of the results of biological investigation to the solution of sociological problems. For, the question of the origin of species has really very little to do with these highly important problems; whilst that of fluctuating variability is intimately and fundamentally bound up with it.

The contrast between these two groups of phenomena, variability (in the strict sense) and mutability, becomes obvious when we imagine that the properties of organisms are built up of perfectly distinct and independent units. The origin of a new unit is a mutation; but the new unit

varies in the degree of its manifestation according to the same laws as those to which the elements of the species, already existing, conform.

The properties of these units can be studied far more conveniently by means of experiments in hybridization than by merely observing or rather waiting for their origin. On the basis of this principle the most complicated phenomena of hybridization must be explained by means of the results of the simplest crosses. For, by a combination of these simpler processes we may expect to arrive at an elucidation of the laws to which the phenomena of hybridization conform, and ultimately be in a position to predict the result in special cases. In this way the application of the theory of mutation to the elucidation of the phenomena of hybridization will enable us to ascertain what conclusions relating to the origin of species the study of these processes may warrant.

A knowledge of the laws of mutation must sooner or later lead to the possibility of inducing mutations at will and so of originating perfectly new characters in animals and plants. And just as the process of selection has enabled us to produce improved races, greater in value and in beauty, so a control of the mutative process will, it is hoped, place in our hands the power of originating permanently improved species of animals and plants.

Hugo de Vries.

Amsterdam, August 1901.

Erratum.

Figure 38, page 191 should read figure 37.

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EARLIER STUDIES AND PRELIMINARY NOTES OF THE AUTHOR.

a. Intracellulare Pangenesis. Jena, 1899.

b. Fluctuating Variability.

Ueber halbe Galtoncurven. Ber. d. d. bot. Ges., 1894, Bd. XII, Heft 7.—Bot. Jaarboek, 1895, VII, p. 74.—Archiv. Néerl., 1895, T. XXVIII, p. 442.

Eenheid in Veranderlykheid. Album der Natuur, 1898.—Revue de l'université de Bruxelles, 1898, T. III, p. 5.—University Chronicle, 1898, I, p. 311.

Alimentation et Sélection. Vol. Jubil. Société biol. Paris, 1899, p. 17.—Biol. Centralblatt, 1900, XX, No. 6.

Othonna crassifolia (L'Othon) Botan. Jaarboek, 1900, XII, p. 20.

c. Mutability.

Over steriele Maisplanten. Bot. Jaarboek, 1889, I, p. 141.

Steriele Mais als erfelyk ras. Bot. Jaarboek, 1890, II. p. 109.

Sur l'introduction de l'Oenothera Lamarckiana dans les Pays-Bas. Ned. Kruidk. Archief, 1895, VI, p. 4.

Sur l'origine expérimentale d'une nouvelle espèce végétale. Cps. rs. de l'Acad. de Paris, 1900.

Sur la mutabilité de l'Oenothera Lamarckiana. Cps. rs. de l'Acad. de Paris, 1900.

Recherches expérimentales sur l'origine des espèces. Revue générale de Botanique, 1901, T. XIII, p. 1.

Die Mutationen und die Mutationsperioden bei der Entstehung der Arten. Vortrag in der Naturf.-Vers., Hamburg, 1901. Leipsic, Veit & Co.

d. After 1901.

Species and Varieties; Their Origin by Mutation, 1st ed., 1905; 2d ed., 1906; Chicago, The Open Court Publishing Co.

Plant-Breeding. Comments on the Experiments of Nilsson and Burbank, 1907. Chicago, The Open Court Publishing Co.

Ueber die Dauer der Mutationsperiode bei Oenothera Lamarckiana. Ber. d. d. bot. Gesellsch., 1905, XXIII, Heft 8.

Die Svalöfer Methode zur Veredlung landwirthschaftlicher Kulturgewächse und ihre Bedeutung für die Selektionstheorie. Archiv für Rassen- und Gesellschaftsbiologie. 3. Jahrg., Heft 3, 1906.

Elementary Species in Agriculture. Proceedings American Philosophical Society, Vol. XLV, 1906, April 18.

Aeltere und neuere Selektionsmethode. Biolog. Centralblatt, Bd. XXVI, Nos. 13-15, 1906.

Die Neuzüchtungen Luther Burbanks. Biolog. Centralbl., Bd. XXVI, No. 19, Sept. 1906.

INTRODUCTION.

INTRODUCTION.

By the Mutation theory I mean the proposition that the attributes of organisms consist of distinct, separate and independent units. These units can be associated in groups and we find, in allied species, the same units and groups of units. Transitions, such as we so frequently meet with in the external form both of animals and plants, are as completely absent between these units as they are between the molecules of the chemist.

It is perhaps unnecessary to remark that these generalizations refer to the animal as well as to the vegetable kingdom. In this book, however, I shall confine myself to the latter, in the belief that the truth of the principle will be granted in the case of the former as soon as it has been shown to apply in that of plants.

The adoption of this principle influences our attitude towards the theory of descent by suggesting to us that species have arisen from one another by a discontinuous, as opposed to a continuous, process. Each new unit, forming a fresh step in this process, sharply and completely separates the new form as an independent species from that from which it sprang. The new species appears all at once; it originates from the parent species without any visible preparation, and without any obvious series of transitional forms.

The Mutation theory affects not only our views on the origin of species but in my opinion bears strongly on the whole question of hybridization. For it shows us that the units with which we deal in hybridization are not the species themselves but the single characters which compose them—the so-called elements of the species. This principle leads to an entirely new method of handling the subject, by enabling us to proceed gradually from the simpler to the more complicated phenomena instead of following the present custom which consists in dealing with the complex cases first.

This work therefore falls into two main parts of which the first treats of the origin of species and varieties by Mutation, and the second of the principles of hybridization.

The Mutation theory is opposed to that conception of the theory of selection which is now prevalent. According to the latter view the material for the origin of new species is afforded by ordinary or so-called individual variation. According to the Mutation theory individual variation has nothing to do with the origin of species. This form of variation, as I hope to show, cannot even by the most rigid and sustained selection lead to a genuine overstepping of the limits of the species and still less to the origin of new and constant characters.

Of course every peculiarity of an organism arises from a previously existing one; not however by ordinary variation, but by a sudden though minute change. It is perhaps appropriate to compare such a change with a chemical substitution.

The name I propose to give to this "species-forming" variability is Mutability—a term in general use before

Darwin's time. The changes brought about by it, the Mutations, are phenomena as to the exact nature of which we understand very little so far. The best-known examples of such Mutations are the so-called spontaneous variations (the "single variations" of Darwin) by which new and distinct varieties arise. They are also termed, fitly enough, sports. In spite of the fact that they occur fairly often, they are usually not noticed until the new form has already appeared, when of course it is too late to study the phenomenon of its origin experimentally. These new forms can be sought for in cultivated species, which are seldom of pure origin; as well as in Nature. But as yet we have no power of inducing them at will.

It is my belief that all the simple characters of animals and plants arise in this way.

The methods of artificial selection correspond to these two types of variability. Ordinary variation, which is also known as individual, fluctuating or gradual variation, is always present; and it can be described in terms of perfectly definite laws which have now been fairly completely formulated. It provides the breeder with material for his improved races. On the other hand he has to deal with Mutations which do not need repeated selection but, at the most, must be kept free from admixture, and which almost always breed true from the first.

Under the general term variation, then, are included two distinct phenomena: Mutability and fluctuation or ordinary variation. The latter forms a suitable object for statistical investigation. The epoch-making researches of QUETELET and GALTON on the anthropological side have raised this study to the position of an independent science. Among biologists, LUDWIG, WEL-

DON, BATESON, DUNCKER, JOHANNSEN, MACLEOD, and others, have been active workers in this field. Fluctuation is either individual or partial: in the former case we are dealing with the statistical comparison of different individuals; in the latter with different but homologous organs of the same individual; for example with the leaves of a tree. In both cases the capacity for variation is regarded by those who are competent to judge as a means of adaptation to the environment. Single organs vary partly in mass and weight and partly in number. The former case is referred to by BATESON as continuous variation; the latter as discontinuous. But these terms are sometimes used by other authors with a different meaning.

The laws of Mutability are quite different from those of individual variation; but, so far as our scanty information reaches they are just as independent of the morphological nature of the mutating organ. We can distinguish between progressive and retrogressive Mutation. The former results in the origin of a new character; the latter in the loss of one already existing. It is, obviously, to progressive Mutation, according to this theory, that the main branches of the animal and vegetable genealogical tree owe their development; but the great majority of the cases of the departure of a single species from the type of the systematic group to which it belongs is due to retrogressive Mutation.

It is to considerations of this kind that the first part of this volume will be devoted. In the first place I shall give a critical revision of the facts on which the theory of Natural Selection of DARWIN and WALLACE and others is based. In the second I shall deal with some examples of the experimental study of new forms.

The experiments to this end were begun in the autumn of 1886 and are now at least in one particular direction almost complete. A description of them will constitute most of the contents of the second part.

The critical revision to which I have referred will form the substance of the first section.

I shall confine my critique to the facts of selection and to the material, afforded by variability, on which selection operates. It will be shown that artificial selection is, as already mentioned, a twofold process. On the one hand it consists in the isolation of constant strains from their neighbors and, inasmuch as the best are chosen, in their improvement. On the other hand it improves races and is the source of those superior fruits which we can only propagate by grafting and other vegetative methods. But this selection, so far as our experience goes, never leads to the origin of new and independent types.

In this first section then it will be our object to render the difference between these two types of variability as clear as possible. A correct apprehension of the nature of this difference will make clear the overwhelming importance of Mutability, as opposed to individual variation, in the production of new species. In connection with this critical treatment I have tried, by experiments on numerous examples of individual variation, to discover the limits to the amount of alteration that can be attained in this way. And we shall see that these are much narrower than a belief in the theory of Selection, as commonly entertained, would lead us to expect.

For the main experiment I have chosen a plant in which I was enabled to follow in detail the phenomenon of Mutation through a number of years. This was

Oenothera Lamarckiana which as long ago as 1886, formed the starting-point of this work. The second part will show that it has not disappointed me, and will give an account of the whole series of Mutations produced by it.

PART I.

THE PRINCIPLES OF THE CURRENT THEORY OF SELECTION.

I. SELECTION AND MUTATION.

In his theory of Selection DARWIN combined two principles relating to the origin of species; and he laid stress sometimes on the one, and sometimes on the other, according to the nature of the available evidence or to the objections of his critics. One was the principle on which the controversy over the origin of species turned in pre-Darwinian days. It was the supposition of a progress by steps in nature, by means of which a new species arose suddenly from a former one. Such a phenomenon was called a Mutation. If the new form was distinguished from its parents by a single character the mutation was obviously a relatively simple process. And those who believed in the "sub-species" always regarded the matter in this simple way, even when they questioned the possibility of such mutations on the ground that they never saw them. This was the attitude of the French school in the middle of the XIXth century. They recognized individual variation, and described it time after time; but they saw no connection between it and the origin of species.

It always seems an extraordinary thing to me that the occurrence of mutations should have escaped the notice of the workers of that time. For they occur both in the cultivated state where they have been called single variations, and also in nature, where as I hope to show

they correspond precisely to the anticipations of the Transmutationists of that time.

The weak point of the whole position before Darwin's time lay in the application of the conception of mutation to the Linnean species, for these are not really elementary species but aggregate ones, and the question of their origin is obviously different from that of their constituent units.

The second principle in DARWIN'S theory was the idea that individual variation could lead to the origin of new species by continued selection. This idea was at that time absolutely new, and found many adherents amongst whom WALLACE, whose views are set forth in his book "Darwinism," must be considered the chief. Moreover it is WALLACE who has insisted that this form of the theory affords the only possible explanation of evolution. He absolutely rejects the theory of the origin of species by mutation. "Single variations" according to him have no significance for the theory of descent.

Experimental researches on individual variability and mutability hardly existed at all at that time. Investigators had to be content with the information of breeders and general biological considerations. But the latter, although they often afford the strongest argument for the theory of descent, seldom distinguish between the two processes in question.

The experience of breeders demands in my opinion the most careful examination before it can be accepted as evidence in a scientific inquiry. Their experiments are neither designed nor carried out with this object in view. A critical revision of the whole range of facts on which the doctrine of selection rests is not only admissible, but is urgently called for. DARWIN accumu-

lated a vast storehouse of facts and observations; but our estimation of the importance and significance of the individual facts themselves has undergone a change. Moreover many new observations have been made which place the results obtained by breeders in a new light.

Breeders with few exceptions do not work in the service of science; and most of them take very little interest in the purely scientific aspect of their work. They do not make the general plan of their experiments as simple as possible in the hope of finding a rational explanation. On the contrary, as a rule, they prefer complex conditions especially where their efforts are directed to the production of new varieties. For the more numerous the factors the greater the expectation of getting something new and good. On the other hand scientific experiments on variability should, where possible, be free from the results of hybridization. But crosses are usually much more important to the breeder than pure races, and only in quite special cases has he the occasion to exclude crossing with the utmost care. Although mutations are often of much greater value to him than individual variations he usually treats them both after the same fashion and often does not even distinguish between them.

Moreover a systematic record of the culture, of the kind that is absolutely essential to work with a scientific object is not kept by breeders. It would cost far too much time and labor. The only records that are kept by most breeders are those which are necessary for the compilation of their catalogues. And if after a few years a new form proves to be something particularly good, its history is written, as I have been personally informed by one of the most distinguished breeders, partly from the information in the older catalogues and partly

from memory in such a manner as best suits the purposes of advertisement. "It goes without saying," he said, "that after three or four years one can no longer remember one's single fertilizations and selections." Many other well-known breeders have expressed themselves to me in similar terms.[1]

If we collect all that is known with absolute certainty about the "How" of the origin of our innumerable garden plants, the result is extraordinarily meagre. Concerning the vast majority of them we do not know any more than that they exist; in the case of others the firm which put them on the market is known, and the year of their introduction; but the names of their raisers are usually kept secret especially where one is dealing with cases in which the crosses have not been performed purposely. And the question as to how the new forms arose, on the answer to which the value of this evidence as bearing on the theory of selection depends, can very seldom be answered. Public statements are dictated by exigencies of advertisement. It is often only found possible to maintain a well-defined improved race on the market by crediting it with further improvement. All such statements therefore require careful scrutiny before they can be utilized as scientific evidence.

I am far from blaming breeders in this matter. It is to friendly intercourse with many of them that I owe in great measure my information on this subject. What I object to is the application by others of the results attained by breeders to questions for which they were neither intended nor devised. It was DARWIN's insight

[1] RÜMKER refers in strong terms to the difficulties which may arise from regarding the grossly exaggerated illustrations in seed catalogues as faithful records of the things depicted. See "*Der wirthschaftliche Mehrwerth guter Culturvarietäten,* 1898, p. 2

which enabled him to build his theory of descent on foundations supplied by breeders. At the same time he left many points untouched, or at any rate undecided, and for the final settlement of such questions I fear that the statements of breeders will seldom suffice.

It is somewhat remarkable that purely scientific investigation has not kept pace with practical experience. This wide field is still open to cultivation, and will, without doubt, some day bear a rich harvest.

It is my object in this section to test the statements of practical breeders, so far as they admit of such criticism. I pay the sincerest tribute to their high practical value especially as in this case science is far behind them. But their application to the theory of descent is another matter. Real service to science can only be rendered by confining oneself to thoroughly authenticated cases.

In conclusion: The analogy between the origin of new forms in nature and in a state of cultivation forms one of the chief supports of the theory of descent. But the *fact* of their origin does not help us to choose between the theory of selection and the theory of mutation; nothing short of a knowledge of the nature and mode of their origin will help us to decide. But on this all-important point the experience of breeders teaches us very little.

I shall try to relate what they tell us in the third chapter of this Part.

II. MUTABILITY AND INDIVIDUAL VARIATION.

§ 1. THE TRANSMUTATION THEORY BEFORE DARWIN.

In the introduction to his "Origin of Species" DARWIN gives a short historical sketch in which he calls

Fig. 1. *Papaver bracteatum monopetalum.*
A. The detached Corolla. B. The whole flower.[1]

attention to the contributions made by his predecessors to the theory of evolution. LAMARCK was the first whose

[1] In the cultures of the firm VILMORIN-ANDRIEUX of Paris there are found every year in the plots of *Papaver bracteatum* single plants whose petals are more or less completely fused. Fig. 1 is drawn from samples which H. L. de VILMORIN was kind enough to send

views on the origin of species attracted general attention. The chief of those who joined him in championing the common origin of all living form was GEOFFROY SAINT-HILAIRE. Their point of view was a purely philosophical one and rested on the principles of natural science current at that time, which sought to account for all natural phenomena without the aid of supernatural causes.

Their followers however entered an entirely different field. They abandoned for the time the investigation of the phylogenetic relationship of all living forms and sought to discover the causes of the relationships of smaller groups.

They adhered almost always to the Biblical conception of creation, and sought to determine which units were created in the beginning. Some investigators regarded the genera as creations, others the species of LINNAEUS, and a third group the so-called "subspecies" which would be much better termed elementary species.

There can be distinguished among DARWIN'S predecessors and contemporaries four different lines of thought characterized by their different attitudes to DARWIN'S theory of descent.

1. The philosophical contemplation of nature by LAMARCK and GEOFFROY SAINT-HILAIRE.

2. The rest of the Transmutationists who regarded the genera as created and the species and subspecies as derived from these.

3. The adherents of the Linnean species, who held that these were created.

4. The so-called school of JORDAN who declared that

me. The plant is not on the market. It is not unreasonable to believe that the appearance of the first ancestor of the whole systematic division of the Sympetalae occurred in geological time in the same way as sympetaly has arisen here as a variety.

the elementary forms which proved themselves immutable when cultivated were the real independent creations.

Let us first consider the views of the Transmutationists.

Before LINNAEUS the genera were regarded as the systematic units and the species were considered as subdivisions of them. Many genera have popular names: these groups were known by the country folk, whilst the species were only in much rarer cases distinguished. TOURNEFORT gave the genera known to him their systematic names; but the species he distinguished only by symbols and not by special names. In his eyes the genera were the essential things, the species merely derivatives.

The view that genera were created in the beginning and that species had developed from them in the lapse of time by transmutation had many adherents. Among them are to be reckoned BUFFON, at least in his earlier works, then BORY DE SAINT-VINCENT, GMELIN, BURDACH, POIRET, FRIES and many others.[1] This view, at one time found an adherent in LINNAEUS.[2] He believed in a simultaneous creation of all forms in Paradise; he suspected however that these forms corresponded to our genera whilst species had arisen from them in part directly and in part by crossings.[3]

This is important because it shows that the modern conception of species did not exist before the time of LINNAEUS or at any rate that it was not the species which

[1] GODRON, *De l'Espèce*, pp. 8-10.

[2] "*Genus omne est naturale, in primordio tale creatum.*" Syst. Nat. Veg. 14. Philos. Bot. No. 159, p. 104.

[3] C. LINNÉ, *Oratio de Telluris habitabilis incremento.* Upsala, 1743; Leyden, 1744.—Idem *Amoenitates academicae.* 1794. T. I., p. 71 (*de Peloriis*).

were regarded as the real units of the system. This is also obvious from the meaning of the expression *nomen specificum* which was in use at that time. TOURNEFORT and his contemporaries wrote after the generic name a short diagnosis each time, in order to distinguish the single species from one another. So long as only a few species were known in each genus, one character sufficed. But as the number of species increased more characters became necessary, until finally many species could only be denoted by a description which occupied several lines. A circumlocution of this kind we now call a diagnosis; then it was called a *nomen specificum* and had to be written out every time one wanted to refer to a particular species.

LINNAEUS substituted his binary nomenclature for these cumbersome *nomina specifica*[1] and, in order to give his species the necessary importance he raised them to the rank of the units of the system. He advanced the proposition *Species tot numeramus, quod diversae formae in principio sunt creatae*[2] and thus laid the foundation of the conception of species that is recognized to-day. And just as it had been supposed up to that time that species arose from genera by natural means, so, according to LINNAEUS, smaller types had arisen from the species.[3] But in order to insure as far as possible the supernatural dignity of his species LINNAEUS forbade his students to study the smaller types: *Varietates levissimas non curat botanicus*, ran the command.[4]

LINNAEUS's species were aggregate species and not

[1] *Philosophia Botanica*, No. 257, p. 207.

[2] *Ibid.*, No. 157, p. 103.

[3] "Varietates sunt plantae eiusdem speciei, mutatae a caussa quacunque occasionali," *Ibid.*, No. 306, p. 243; No. 158, p. 104.

[4] *Ibid.*, No. 310.

true units. It seems that LINNAEUS himself was fully aware of the fact, but it is certain that it was gradually lost sight of by his followers. In relatively few cases did he himself distinguish varieties within his species, and it is well known that when he did they were often raised to the rank of species by those who followed him. Well-known examples are afforded by *Primula veris L.* with the three varieties *vulgaris* (*acaulis*) (Fig. 2), *elatior* and *officinalis*,[1] which are now universally regarded as species solely on the authority of JACQUIN without any further justification. In like manner *Lychnis dioica L.* split up into *L. diurna* and *L. vespertina*, *Platanthera bifolia L.* into *P. bifolia* and *P. chlorantha* and so forth.

Fig. 2. An umbel of *Primula acaulis*.

Numerous examples of a similar kind will occur to the reader. Conversely also Linnean species have been degraded to the rank of varieties: for example the Index Kewensis which recognizes the Primula species of JAC-

[1] *Primula acaulis* is distinguished from the two other subspecies by the fact that its flowers arise singly by their stalks from the axils of the leaves and are not united to form an umbel. This species occurs in certain localities in the Netherlands, in the wild state, and from time to time bears umbels of which one is drawn in Fig. 2. Such cases are regarded as atavistic, as reversionary to some common ancestor of those Primulas which still possess umbels. But this atavism is not considered by the best systematists as sufficient ground for re-constituting *P. acaulis* as a variety and the main species *P. veris* as a species, in systematic works. From the point of view of the estimation of the systematic value of Atavism in general this case evidently is of much importance.

QUIN regards *Datura Tatula L.* as a variety of *D. Stramonium L.*[1]

LINNAEUS' *species,* therefore, embraced his varieties and these *varietates minores,* which he would not allow his pupils to investigate. But it was not proved that all these smaller types had arisen from the species; it merely followed from his definition of species. And so long as the Linnean species of the systematists provided them with sufficient work there was no reason for them to doubt his words or disregard his precept. But as the study and description of the "species" particularly of the European Flora gradually approached completion the attention of naturalists inevitably turned in the direction of the hitherto neglected *Varietates minores.*

It soon became evident that these were much more numerous than LINNAEUS ever supposed; moreover, that they were distinguished by just as numerous and just as definite characters as Linnean species. Their discoverers demanded for them the "rank" of Linnean species and elevated them to it. Some authors went so far as to assert that by such discriminations they had created new species.

The best known example is afforded by *Draba verna* which has been studied carefully by JORDAN and by many other independent investigators after him. Among the latter I would mention DE BARY whose results, which are in full agreement with JORDAN's were published after his death, by F. ROSEN in the Botanische Zeitung for 1889. The European Flora includes about 200 (elementary) "species" of Draba which together constitute the old species *Verna* and, so far, have remained constant

[1] It is most remarkable that in the *Index Kewensis* which was published at DARWIN's expense after his death no distinction is drawn between varieties and synonyms.

and distinct under cultivation. The extent of these differences is sufficiently indicated by a series of the most important forms, in Fig. 3.

A heated controversy in which JORDAN and GODRON played the most prominent parts has raged over the ques-

Fig. 3. Subspecies of *Draba verna*. 1. *D. violacea*; 2., 3. and 4. *D. scabra*; 5. *D. subnitens*; 6. *D. majuscula*; 7. *D. obconica*; 8. *D. glaucina*; 9. *D. elongata*; 10. *D. graminea*. (After F. ROSEN, Bot. Zeitung, 1889. Plate VIII.)

tion as to whether these smaller perfectly circumscribed types should be called species or not. JORDAN and the advocates of the smaller species based their views on the results of cultures; and in this way they have en-

riched science with a collection of experimental facts of the greatest importance. A considerable portion of the fourth chapter of this work will be devoted to a critical consideration of these facts.

Fig. 4. Subspecies of *Viola tricolor.* 1. *V. agrestis*; 2. *V. segetalis,* general habit similar to that of *V. agrestis*; 3. *V. gracilescens;* 4. *V. pallescens;* 5. *V. nemausensis.* (After A. Jordan, *Observ. s. plusieurs plantes rares ou critiques,* II, 1846. Plates 1 and 2.)

The description of any form as a species, or rather the supposed proof that any form *was* a species, carried

with it the assumption that the form under consideration had been created as such. The reasonableness of this position was recognized by both parties but especially by GODRON and JORDAN. But at the present day when the common origin of all species is hardly ever called in question it is very difficult to judge this controversy fairly.

The origin of a new form from another was termed at that time a mutation.[1] GODRON and JORDAN asserted that every one of the forms constituting their species was immutable. JORDAN moreover tried to prove the truth of this statement by breeding experiments. He recognized individual variation and observed and recorded it accurately.[2] He was also acquainted with local races[3] whose differences disappear whenever they are cultivated for a few years next one another in the same soil; he knew moreover that as a rule it took only a few generations to effect this change. Further, he was familiar with the results of accidental crosses by insects or wind, and mentioned the genera (*Cirsium* etc.) in which this was most apt to occur.

But individual variability and mutability were absolutely different things in his eyes; he frequently observed the first; but never saw an example[4] of the latter. That was why he held species to be immutable.[5]

[1] Already LAMARCK used the terms *"races mutables ou variables"*; see GIARD, *Discours d'ouverture de J. B. Lamarck,* 1907, page 111 (Note of 1908).

[2] A. JORDAN, *De l'origine des arbres fruitiers,* 1853, p. 9.

[3] *Loc. cit.,* p. 10

[4] Besides the common *Viola tricolor, V. arvensis* (MURRAY) is very familiar; it is reckoned by many authors as belonging to the same species. Compare for example KOCH, *Synopsis Florae germanicae et helveticae. V. arvensis* itself consists of a series of constant forms of which our Fig. 4 shows some of the more important.

[5] JORDAN, *De l'Origine des arbres fruitiers,* 1853. In this work and in the other essays Jordan always uses the words *"mutation"* and *"immutabilité"* where he is dealing with the supposed change of

Godron also distinguishes quite clearly between specific characters, and trivial fortuitous and purely "individual" deviations which soon disappear when the conditions which called them forth cease. The latter are united together by a series of transitions; the former are not.[1]

When Darwin's work on the origin of species appeared,[2] the controversy over the ideas of species and mutability raged most fiercely in France. But it only turned on the question whether the larger or the smaller species were separately created, or whether they had both arisen from an original type. This original type, however, was never thought of as being larger than a genus.[3] The transformation or transmutation theory of those days was therefore an entirely different thing from the modern theory of descent. Nevertheless Darwin himself says in 1858 at the suggestion of Lyell and Hooker he resolved to write a book on the "Transmutation" of species, a book which was published in the following year under the title of the Origin of Species.[4]

It is curious that the terms Mutation, Mutability, Immutability and so forth should have been so completely driven out of use by the theory of Selection. Darwin directed his whole energy with full knowledge against the dogma of the immutability of species. His "Origin of Species" begins with the statement that until recently the great majority of investigators had believed "that species were immutable productions."[5] "I had become, in the year 1837 or 1838, convinced that species were mutable productions,"[6] says he in his Autobiography;

one species into another. See pp. 7, 9, 11, 13, 34, etc. Also Godron, *De l'Espèce*, e. g., II, p. 422.

[1] Godron, *De l'Espèce*, I, p. 175. [2] Nov. 24, 1859.
[3] See Wallace, *Darwinism*, pp. 3-6. [4] *Life and Letters*, I, p. 85.
[5] *Origin of Species*, 6th ed., 1898. *Historical Sketch*, p. xiii.
[6] *Life and Letters*, I, p. 93.

and in the passage cited in the Origin, he discusses the question whether in Paleontology the immutability of species was or was not assumed by the most prominent workers.[1]

The prevailing opinion was that individual variability and mutability were two distinct phenomena. Variability was well known both in cultivated and in wild species, but most thoroughly in wild species which had been kept in cultivation through a number of years. It was found however to be limited, to depend upon the influence of the environment and to be useful as a means of adaptation. Mutability was not encountered in practical experience. No cases of a species arising from another had occurred in scientific cultures, nor were there any sufficiently authenticated instances of the origin of new forms in the nursery or the farm in spite of a thorough and critical scrutiny.[2]

The adherents of the Transmutation theory explained the systematic relationship of the single forms (species, varieties, and so forth) within the genera by the theory that they had a common origin. The opponents of this theory, in so far as they were upholders of the Linnean conception of species, held exactly the same views, except that they regarded the species as created and not the genera. Foremost amongst them was Godron, who considered the races and varieties and even the species of Jordan as having arisen from the Linnean species by natural means, and made a very extensive collection of facts and observations to prove this view.

The third school was sharply opposed to these two groups, the Transmutationists and the upholders of the

[1] *Origin,* p. xviii.

[2] Jordan, *De l'Origine des arbres fruitiers,* 1853, and Godron, *De l'espèce et des races.*

Linnean conception of species. It relied exclusively on the Biblical story of creation and on experiment. Every form which proved itself to be immutable by experiment was, according to their theory, an independently created form. The experiment consisted in cultivating the particular form in a garden for a few generations. They disapproved of the systematic grouping together of such pure forms into larger "species" on the ground that it was artificial and arbitrary. They recognized genera and the larger groups as necessary, but regarded them as manifestly artificial divisions.

According as one belonged to the one or the other of these parties one was more or less prepared for DARWIN's new teaching. The thin ranks of the Transmutationists and the huge Linnean army admitted *a priori* the origin of races, varieties and JORDAN's species from other forms, and this in spite of the complete absence of experimental proof. It was against these that DARWIN turned his energies to show, what was indeed the chief object of his argument, that the supposition of a common origin for genera and families was as much justified as the view held at that time, that the forms gathered together in one species were descended from a common ancestor.

The adherents of JORDAN's school who regarded the elementary species as created, were least prepared for DARWIN's teaching. There were however very few of them, and their system, by being so rich in species (*Draba verna* alone falls into more than 200), stood very much in the way of a wide acceptance of their views. At any rate they were not, or at most only very slightly, convinced by DARWIN; the bulk of them maintained their original position. The only one of them that I would

mention here is MICHAELE GANDOGER whose Flora Europae is the most comprehensive work along this line of research.

The controversy before the time of DARWIN had therefore led to two essentially distinct results. These were:

1. The experimental proof of the existence of numerous, constant and mutually independent types within the limits of the Linnean species.

2. The general conviction that these constant types had arisen naturally from larger groups or species by mutation.[1]

§ 2. DARWIN'S SELECTION THEORY.

The theory of Descent aims at the scientific explanation of systematic relationship. It is DARWIN's immortal service to have obtained general recognition for this generalization. By doing this he revolutionized the whole of biological, systematic, embryological and paleontological science, tapping inexhaustible sources for new investigation and discovering everywhere mines where new facts were to be had for the picking up.

The several propositions and hypotheses which DARWIN employed as supports for this theory should be regarded now only as such, since their interest is mainly historical. They have served their purpose and are thereby fully justified. Whether they contain in part what is unproven or what is incorrect matters not. But they contain, over and above that, a large mass of important facts which can be made use of to build further

[1] The terms immutability and so forth have not entirely dropped out of use. E. g., B. J. COSTANTIN, *Accomodation des plantes aux climats froid et chaud*, Bull. Scientif.,publié par ALFRED GIARD, T. 31, p. 490, 1897, and BATESON, *Materials for the Study of Variation*, 1894, p. 2.

on the foundations laid by DARWIN. This is especially true of the theory of selection, which now has served its time as an argument for the theory of Descent; happily this theory no longer stands in need of such support. We are now concerned to bring the origin of species into the field of experimental investigation. The position of the theory of Descent as a comparative science is completely assured by the results DARWIN obtained; but as an experimental science it has made feeble progress.[1]

The cause of this lies in my opinion not so much in the difficulties of the investigation as in the lack of definiteness of this part of the theory. In the systematic sphere the discoveries could have been predicted; this was far from being the case on the physiological side.

DARWIN was never quite clear about the physiological part of the theory of Selection. It seems to me that he always inclined first in one direction and then in another, never fully deciding between the two views. In his earlier works especially, he treated spontaneous variations (single variations) as the material afforded for natural selection whilst in his later works, in consequence of the objections of his critics he gave greater prominence to the part played by individual variation in the production of new species. But he never sharply discriminated between these two processes. Moreover, such a discrimination was not in the interests of his main object. It would have led him to many difficult points whose solution was not necessary to the theory of descent, and would have diverted attention too much from the main point at issue.

As we have seen in the foregoing section, the

[1] See also BATESON, *Materials for the Study of Variation*, pp. 7 and 11.

proposition that races, varieties and subspecies of wild as well as of cultivated plants have arisen by certain modifications from "species" received general recognition. DARWIN had collected all the facts available for a history of these changes in the case of cultivated plants.[1] They provide us with a history of garden plants and often also give the source and the date of introduction of varieties, but they do not tell us whence they came or how they arose.[2]

"Varieties are incipient species" and *"species have descended, like varieties, from other species"*; these are the two famous propositions which DARWIN is continually asserting and with whose proof he is chiefly concerned.[3] In other words: the origin of varieties from species is granted; why not species from species? In order to prove this it is obviously not necessary to know the exact way in which varieties themselves originate. It is sufficient that the relation between species and genera is the same as that between varieties and species.

DARWIN asserts again and again that it must not be forgotten that under the term of variations mere individual differences are included.[4] His variability is therefore always to be understood in a double sense. It consists on the one hand of individual differences and on the other of single variations.[5] The former belong to those phenomena which we now term individual varia-

[1] Of later works compare especially ALPH. DE CANDOLLE, *Sur l'origine des plantes cultivées.*

[2] See also BATESON, *Materials,* p. 17.

[3] *Origin of Species,* 6th ed., pp. 2, 4, 86, etc.

[4] *Origin,* ibid., pp. 64, 80, etc.

[5] *Life and Letters,* III, p. 108. As examples of single variations are considered such cases as the color of the flowers of *Datura Tatula* (a blue form belonging to the white-flowered *D. Stramonium*) and the absence of spikes on the fruits of *Datura inermis.* See Fig. 5.

tion, and conform to QUETELET's law. The latter are sporadic, spontaneous changes corresponding to our Mutations (Fig. 5).

DARWIN almost always speaks of these two types in his discussion on Selection but never separates them, and is always in doubt as to their relative importance in the origin of species.

Fig. 5. 1. *Datura Tatula,* with blue corolla and foliage tinged with red. 2. Fruit of *D. Stramonium* with thorns, unripe. 3. Fruit of *D. (Stramonium) inermis,* without thorns, ripe, dry and open.

This being the case, it seems to me that it is almost unfair in a criticism of DARWIN's views to regard these two types as distinct. If I do so, I do it with the express object of showing that although DARWIN was acquainted with the two phenomena he was not prepared to separate them completely on the basis of their significance for

his theory. Here, as everywhere, DARWIN advanced with the utmost caution.

Our problem then is this: In the formation of new species, does natural selection choose the extreme variants of the ordinary individual variation, or does it choose occasional Mutations. In any large community there is always an abundant supply of extreme variants. Moreover the struggle for existence does not preserve the single absolutely perfect ones only, but groups of the best, since it simply eliminates the least perfectly adapted. There is, so to speak, always plenty of material for selection in every species, and in every character. But individual variability is, as far as our experience goes, by no means unlimited; its limits are not indeed precise, but they fall well within the range of QUETELET's Law.

Single variations are chance phenomena into whose essential nature we have as yet no insight. We know that they occur and that they occur seldom; but not too seldom. As to how they come about scarcely anything is known, but it is generally assumed that they appear suddenly,[1] and they are consequently termed sports. They suddenly change a species into a new form; or, from a variety, they make a new one absolutely different. Frequently they concern only a single character and then usually consist in the loss or latency of a character already present, e. g., white flowers, absence of thorns (*Datura inermis,* Fig. 5), hairs, runners (e. g., *Fragaria alpina,* Figs. 6 and 7, pp. 33 and 34),[2] seeds, branching,

[1] By far the majority of observations that have been adduced as instances come under the heading of hybridization.

[2] The GAILLON strawberries (Fig. 7) which are distinguished from the ordinary monthly strawberries (*Fragaria alpina,* Fig. 6) solely by the absence of suckers and the correspondingly greater branching of the rosettes are often cultivated for the very reason of

etc.; these cases are instances of retrogressive mutability and have no signification for the elucidation of the main lines of descent.

Apart from this quite definite group of modifications by loss, single variations seem to be presented by all characters, to proceed in every direction and to be apparently without limit. To sum up, individual differences are always present, occur in every direction and in every character, but are limited and conform to definite laws. Single variations, on the other hand, are sporadic phenomena, appearing only from time to time, and suddenly changing

Fig. 6. *Fragaria alpina,* Monthly Strawberry. (Fraisier des quatre saisons.)

the forms of life. They cannot be induced at will, but must be waited for.[1]

We have thus to decide between:

1. a selection of extreme variants.

2. a selection of mutants.

The question for Darwin was, which of these two has played the greater part in the origin of species?[2]

this deficiency. See VILMORIN-ANDRIEUX, *Les plantes potagères,* 1883, pp. 221-222.

[1] *Origin,* loc. cit., p. 62.

[2] The selection of extreme variants in nature forms the so-called local races and plays an important part not only in acclimatization but especially in many cases of adaptation to new environmental conditions. See III, § 4.

The breeder employs both, according as opportunity offers. DARWIN asserts over and over again that their method consists in the accumulation of successive slight variations.[1] But as to whether these small changes are variations or mutations he gives no decision. Natural selection, he says, like artificial, chooses these "*slight variations*,"[2] but to which category these severally belong is left uncertain. Moreover it was DARWIN's belief that Natural Selection was not the sole factor, for at the

Fig. 7. *Fragaria alpina*, Monthly Strawberry without runners. (Fraisier des quatre saisons sans coulants, Fraisier de GAILLON).

conclusion of the introduction to his Origin he says, "*I am convinced that natural selection has been the most important, but not the exclusive means of modification.*"[3]

In almost all works on DARWIN's theory we find the story of how he arrived at his theory of selection by reading MALTHUS's Essay on Population.[4] Already well

[1] *Origin*, loc. cit., pp. 3, 63, 64, etc.
[2] *Ibid.*
[3] See also *Origin*, p. 72.
[4] See *Life and Letters*, I, pp. 83, 84.

acquainted with the struggle for existence and the unceasing destruction of countless individuals, he found in that book the long sought solution. He came to the conclusion that selection played the same part among animals and plants as it does amongst mankind, and that in this manner species may have arisen. This conclusion, however, is simply the idea of a genius and does not directly follow from MALTHUS's work. It has become one of the main supports of the doctrine of descent. But it was to the genius of the great thinker, not to the soundness of the raw material that the magnificence of the result was due.

In the light of what we know now[1] this story of the origin of the theory of selection often stands openly contradicted by DARWIN's own view. Natural selection, says he, works on *"chance variations."*[2] *"Unless such occur natural selection can do nothing."*[3] From such utterances it is clear that DARWIN attributed a very great and often preponderating, perhaps even an exclusive, significance to *"single variations."* For individual variability always provides natural selection with the required material in the form, sometimes of greater and sometimes of less deviations from the type; it is, moreover, exhibited everywhere and in all directions. This fact was known quite well at that time, and DARWIN himself was quite clear about it. But the laws formulated later by QUETELET were not known; and the general insight into the matter was much less deep than it is at present; no one however questioned the universal occurrence of

[1] It was in 1838 that DARWIN read MALTHUS's book, and QUETELET's *Anthropométrie* first appeared in 1870.

[2] *Life and Letters,* II, p. 87, etc.

[3] *Origin,* p. 64, etc.

variability. The chance variations were not therefore the extreme variants of the ordinary variability; they were sporadic occurrences. Natural selection is on the lookout for these, says DARWIN, and seizes on them "*whenever and wherever opportunity offers.*"[1]

DARWIN regarded these occasional deviations, these mutations, as appearing from time to time and in a general way conforming to definite laws as yet imperfectly understood. According to these laws it could not happen that any considerable length of time should pass by without the appearance of at least a few considerable variations of this kind. To such variations would be due the progress which the majority of living forms exhibit in the course of the centuries. The longer the time the better is the prospect of the appearance of favorable variations,[2] especially if these should only appear very seldom.[3] They provide us with "intermittent results."[4]

Moreover DARWIN went so far as to believe in a certain periodicity. "Nascent species are more plastic," that is to say produce more sports and have therefore a better chance of splitting up into new species. DARWIN cites NAUDIN and HERBERT as the authors of this view, which they had derived from their comparative studies of the forms occurring within certain groups of plants.[5] SCHAAFHAUSEN[6] mentions the unequal rate of the progress in different branches of the genealogical tree, in some of them the changes taking place very quickly whilst in others absolute stagnation seemed to be the rule during long geological epochs. To produce a genuine new species, a variety must from time to time, perhaps at long

[1] *Loc. cit.*, pp. 65, 66. [2] *Ibid.*, pp. 82, 86. [3] *Ibid.*, pp. 85, 92
[4] *Ibid.*, p. 85. [5] *Ibid., Hist. Sketch*, p. xix. [6] *Ibid.*, p. xx.

intervals, give off variations in the same direction. In this way it progresses "step by step."[1]

Let us look for a moment at DARWIN's views on the influence of external conditions. On this matter again we find that his opinion is by no means fixed. Sometimes he would appear to think that it has played very little part in the origin of species, at other times he ascribes great significance to it. And inasmuch as he was quite familiar with the relation of individual variation to the environment, it follows that he was chiefly concerned here with single variations. In a letter to HOOKER, 1856, he says, "My conclusion is, that external conditions do *extremely* little, except in causing mere variability." "How much they do is the point of all others on which I feel myself very weak."[2]

We are all familiar in the pages of DARWIN's books with the important rôle ascribed to changed conditions of life. Especially in the case of the transport of a plant from one climate to another and the effects of the first years of cultivation on a wild species.[3] Species therefore with a wider geographical distribution are more likely to produce new forms.

In later years DARWIN has again changed his views on this point; after reading HOFFMANN's famous researches he said: *No doubt I originally attributed too little weight to the direct action of conditions. Perhaps hundreds of generations of exposure are necessary. It is a most perplexing subject.* (1881.)[4]

The strongest influence on DARWIN in his relation to this question was that produced by a criticism which was published in 1869 by FLEEMING JENKIN in the

[1] *Ibid.*, p. 66.
[2] *Life and Letters*, II, p. 87.
[3] *Origin*, p. 64, etc.
[4] *Life and Letters*, III, p. 345.

North British Review.[1] This writer tried to prove, by calculations, that the likelihood of single variations maintaining themselves in the struggle for existence or of ultimately being victorious in it was very faint. DARWIN allowed himself to be convinced by this and says forthwith: *I always thought individual differences more important, but I was blind, and thought that single variations might be preserved much oftener than I now see is possible.* As the result of this criticism he made many alterations in the subsequent editions of the Origin.

Finally I shall refer to the conclusion which DARWIN derived from his theory of Pangenesis in its relation to these two forms of variability.[2] There are two absolutely different groups of causes. First, the relative number of the units, their activity, their inactivity, their relative positions and the calling to life of those long inactive. Such changes occur without the units themselves being modified by them. *Such changes will amply account for much fluctuating variability,* that is for that kind of variability which we now call individual, gradual or fluctuating variability.

The second group of causes includes the direct effect of altered conditions on the organization of the individual, in which case DARWIN supposes the units themselves to be altered. If the new units have then sufficiently multiplied, to be a match for the units already existing they will lead to the elaboration of new structures.

These quotations convince me that DARWIN believed the main branches of his genealogical tree to have arisen by a modification of his gemmules and that he regarded

[1] *Origin,* p. 71. *Life and Letters,* III, p. 108.

[2] *Animals and Plants under Domestication.* 2d ed., 1875, II, p. 390.

fluctuating variability as a phenomenon of an entirely different kind.[1]

To sum up, we see that DARWIN always distinguished between individual differences and single variations and that he ascribed to the latter at least a very considerable rôle in the origin of species. It was only by the pressure of criticism that he finally gave up this view and gave the place of honor to the ever present individual variations.

§ 3. WALLACE'S SELECTION THEORY.

In his book on "Darwinism" ALFRED RUSSEL WALLACE has collected in an excellent and convincing manner a valuable mass of evidence for the theory of descent.[2] Few authors except DARWIN have taken such a prominent part in fighting for this theory, as he. His book "Darwinism" consists essentially of two parts. In the first sections WALLACE deals with variability and selection, in the second he describes the wonderful adaptations of animals and plants to their environment and seeks to explain them on the basis of DARWIN's theory by bringing out as forcibly as possible the agreement between the demands of the theory and the facts themselves. This latter half is undoubtedly the most interesting of the whole work. But I shall only discuss his theory of selection in this book.

WALLACE's selection theory differs from that of DARWIN in one essential point. WALLACE regards the ever present individual variation as the material from which natural selection forms new species. It is his main

[1] See also my *Intracellulare Pangenesis*, pp. 73-74, 210, etc.

[2] A. R. WALLACE, *Darwinism, an Exposition of the Theory of Natural Selection with Some of its Applications.* London, 1889, 2d. ed.

object to show *that animals and plants do perpetually vary in the manner and to the amount requisite.*[1] Single variations he regards as absolutely without significance; they have played no part (he says), or at most hardly any, in the origin of species.[2]

Our author holds himself to be at one with DARWIN in essentials and only to have rendered his selection theory sharper and more precise. The hosts of doubts which, as we saw in the preceding section, were always so carefully brought forward and discussed by DARWIN, disappear. The theory has become a compact, clear and surprisingly simple one. WALLACE takes just as careful account of the systematic and biological facts as DARWIN did in his cautious way, but WALLACE's theory is much more convenient and attractive than DARWIN's.

This very clearness in the mode of presentation makes it easy for the critic to discover the weak spot. In fact the author himself almost lays his finger on it. At the end of the first section he gives a summary of his collection of facts and the method of his proof; and one has only to follow carefully to discover the weak point in his argument.[3]

It will be useful to recapitulate as briefly as may be this argument.

WALLACE's theory of natural selection rests on two series of facts. The first is the rapid multiplication and the resulting premature death of innumerable individuals. The second is variability and the survival of the fittest. Against this part of his argument I have no objection to raise. He then goes on to consider another important

[1] *Darwinism*, 2d. ed., p. 13.

[2] "My whole work tends forcibly to illustrate the overwhelming importance of natural selection." WALLACE, *loc. cit.*, pp. vii-viii.

[3] *Darwinism*, pp. 12, 13.

point. This point concerns the principle of the inheritance of variations and the artificial improvement of races by selection. In many cases cultivated forms have become so different from their wild ancestors by this means, that they can scarcely be recognized as their descendants. But the word races has evidently a double signification. It means not only the races improved by selection, but also the constant subspecies of unknown origin which already exist.[1] Without doubt many cultivated forms diverge to a certain extent from the species to which they are considered to belong by systematists. But these forms are subspecies and their common origin from a single species is just as good a hypothesis as that of the common origin of the species of a genus. Cultivated subspecies are in well-known cases older than cultivation itself; as WALLACE himself for example shows in the case of the races of the dog.[2] How they have arisen we do not know, not even in the case of those that have probably arisen in a state of domestication.

On this slender foundation WALLACE now proceeds to build further, and says, p. 12: *"It is therefore proved that if any particular kind of variation is preserved and bred from, the variation itself goes on increasing in amount to an enormous extent; and the bearing of this on the question of the origin of species is most important."*

But this thesis is by no means proved; on the contrary its truth is only assumed for the sake of the argument both by DARWIN and WALLACE, and by the mass of their followers.

WALLACE evades this point in his book; he neither

[1] As for instance the races of mankind.

[2] *Loc. cit.*, p. 88.

subjects it to a stringent criticism nor does he devote a separate section to it. Furthermore in the treatment of single instances this thesis is taken for granted without further proof. One sees this most clearly in the discussion of the apple:[1] It is known, he says, that all our kinds of apples spring from the wild Pyrus Malus and that from this over a thousand different forms have been developed. This gives one the impression that cultivation produced these numerous forms. But as a matter of fact the apple in the wild condition is a polymorphous species rich in subspecies and the well differentiated types which are now cultivated already exist among the wild forms. The transformation of the wild crab apples into juicy and finely flavored fruits is all that has been brought about by cultivation.

It is an absolutely unproved assumption that individual variation extends its range by selection and increases "*to an enormous extent.*" This is the weak point in WALLACE'S selection theory.

I admit that with this assumption it would be very easy and simple to account for the phenomena of adaptation, and that this forms a very strong argument for it. And if it were only a matter of this explanation little purpose would be served by raising objections to it.

But it is, as a matter of fact, fallacious. Selection certainly leads to enormous practical results, but that is a very different thing from enormous biological changes. The fact that a man can increase the yield per acre by one-half, has no significance from the point of view of the origin of species. In the third chapter I shall seek to prove this by the help of facts.

It is not necessary to follow WALLACE'S argument

[1] *Loc. cit.*, p. 87.

further. If his assumption is once granted everything else follows. On page 13 he again sums up his position. He is concerned there to show that variations of every kind can be increased and accumulated by selection not only in the cultivated but in the wild condition. I fully admit that WALLACE has effected this proof in a masterly and convincing manner. But we also require proof that this increase and accumulation takes place "*to the amount requisite*" for the origin of new species and subspecies; and this proof WALLACE neither brings forward nor seeks. Instead of it, his book is full of instances of the compound nature of cultivated and of wild species and of their so-called elementary or subspecies;[1] but how these have arisen we are not told. He has equally little success in proving that races which have arisen by selection remain constant without further selection.

Finally, we see that WALLACE in his selection theory starts from individual or ordinary variability and allows no share in the process to single variations. He shows that the hypothesis thus simplified effectively coordinates systematic and biological facts, but he fails in proving that as a matter of fact specific characters can really arise by the selection of individual differences.

§ 4. THE VARIOUS FORMS OF VARIABILITY.

Nothing is more variable than the meaning of the word variability. Many authors use this word in so comprehensive a sense that one cannot understand what they mean. (Fig. 8.)

It is therefore important to distinguish as clearly as possible between the various phenomena included under

[1] See for example pp. 77-78, 85-86, etc.

this term. For they stand in absolutely different relation to our thesis.

The following groups of phenomena usually fall within the meaning of the term variability:

Fig. 8. *Hedera Helix var. arborea.*[1]

1. Systematic polymorphism and its supposed causes.
2. Polymorphism caused by crossing.

[1] The best known example is afforded by *Hedera Helix arborea* which is offered by many nurserymen as *var. arborea.* It is not a variety, but consists simply of the erect flowering shoots cut off the ordinary ivy, stuck in the ground, and grown as trees. In April 1888 I made some such cuttings, and have cultivated the best one till the present time. It forms a richly branched bush over a meter high (Fig. 8). As is shown in the figure at a, b, c, creeping branches arise from time to time. In 1893 I sowed the berries of an older plant of this kind, in this case an ivy bush of about two meters, and obtained over a thousand seedlings. These still grow in our garden and have made,up till now, exclusively creeping stems and branches. The *Arborea*-form is evidently not inherited. Similar phenomena occur in many other genera, for example in the creeping species of figs in South Europe; but they have not been sufficiently investigated.

3. The differences, in individuals and organs, which follow QUETELET's law.
4. The so-called spontaneous variations.

The special problem which the mutation theory seeks to explain is the manifold diversity of specific forms; spontaneous variations are the facts on which this explanation is based. The truth of this explanation will then be tested by its application to hybrids; and, if possible, proved. Individual variability however will be shown to be of only secondary importance.

It will be convenient to deal with these groups one by one.

1. *Systematic Polymorphism and its Supposed Causes.*

Linnean species are aggregate species. They include sometimes a small but often a large series of forms which are as sharply and completely distinguished from one another as are the best species. These lower-rank forms are usually called varieties or subspecies; varieties, if they are characterized by a single striking character, but subspecies if they are distinguishable by the sum of their characters, by their so-called habit. But on this point there is a great diversity of opinion. Some authors regard all these special forms as elementary species and consequently give them double names, thereby breaking up the Linnean species. It is well known that in this way *Draba verna*[1] and *Viola tricolor*[2] and many other old species have been broken up (in the case of *Draba verna* into 200) smaller groups of perfectly distinct and usually local elementary species. By experiment and culture these forms prove constant, they do not change into one another, nor do they reproduce the typical or general form of the species. The majority of varieties

[1] See Fig. 3 on page 22. [2] See Fig. 4 on page 23.

are just as constant as these. Whether we give them binary and ternary names is not of much consequence. It has always been assumed both before and after DARWIN's time, that they have a common origin, but in remarkably few cases is there historical evidence that this is so. When and how *Datura Stramonium inermis, Robinia Pseud-Acacia inermis, Lychnis diurna glaberrima*, and the whole series of glabrous thornless, white-flowered, laciniate forms, and so forth, have arisen we do not know. They exist and claim recognition equally with the best species. There are a few exceptions, for example *Chelidonium laciniatum* Mill. (Fig. 37 in V, § 25), *Fragaria alpina* Gaillon (Fig. 7, p. 30), etc., whose source is known.

In practical horticulture matters are just as bad. Endless varieties are known but only in rare cases is there any historical information as to their origin.[1]

This section of the subject of variability therefore is a purely comparative one, its laws are morphological, and only rarely does it lend itself to historical or experimental study.

2. *Polymorphism induced by hybridization* is due to new combinations of the heritable characters of the forms crossed. Two groups of phenomena must be distinguished here: scientific experiment and horticultural and agricultural crosses. The scientific investigator chooses, if he can, the least "variable" species whilst the gardener prefers to cross types of which at least one is very "variable." For this variability can be inherited by the hybrid and increases the likelihood of getting new forms; and this is of course

[1] (Note of 1908.) A most interesting and complete list of these instances has since been given by KORSCHINSKY. See *Flora*, 1901, Bd. 59, pp. 240-363.

what is wanted. New elementary characters arise in hybridization experiments solely through this kind of variability, and not as the result of the crossing itself; as for example ALFRED BLEU, the distinguished raiser of Caladiums, has assured me to be the case with his cultures.

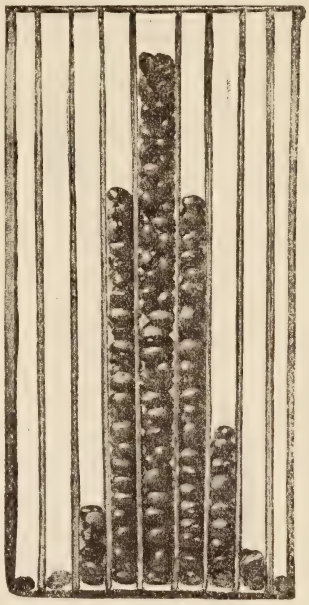


Fig. 9. Glass Jar with Beans.[2]

3. *Variability in the restricted sense or individual variability,* is the name given to those dissimilarities of individuals and organs, which can be described in terms of QUETELET'S laws.[1]

These laws, with which DARWIN was not familiar, and which were only imperfectly dealt with by WALLACE, have since that time been the subject of close investigation; with the result that it has become increasingly evident that these varia-

[1] See Figs. 9-13; also Fig. 22 (curve of 40,000 beets) in chapter 3, § 11, where also the theoretical curve is shown.

[2] Case containing beans to demonstrate their variability in length. The glass case is divided by strips of glass into nine equal partitions. About 450 beans (redspotted seeds of *Phaseolus vulgaris*) were picked from a bought sample and the individuals measured. Their length varied between 8-16 millimeters, and in the following proportions:

Partitions	1	2	3	4	5	6	7	8	9
mm.	8	9	10	11	12	13	14	15	16
number	1	2	23	108	167	106	33	7	1

The beans were then placed in the subdivisions of the jar, in such a way that each compartment only contained beans of the same length (measured in whole millimeters) and in the order shown above. Without further treatment the beans show a grouping ac-

tions are of an entirely different nature from the rest of the phenomena included under the name of variability. They have this in common that they are always present and can be observed every year and in every group of

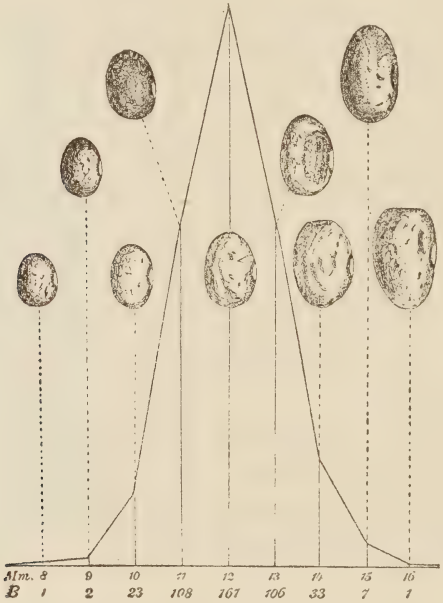


Fig. 10. Curve of Beans.[1]

individuals provided it is not too small. They are always grouped round a mean, and the numbers of the deviations

cording to Quetelet's law. For a more exact demonstration a correction would be necessary, since obviously the larger beans fill up their compartment more than a similar number of small ones.

[1] Curve of the red-spotted beans. The curve is plotted from the observations reproduced in Fig. 9. It corresponds to the theoretical form $(a+b)^n$ sufficiently exactly, as is evident by mere inspection. The length of the ordinates is proportional and almost equal to the corrected height of the groups of beans belonging to each compartment of the glass case. The number of beans found in each compartment is found at the foot of the corresponding ordinate. A bean from each group is drawn as a sample to show the extent of fluctuating variability in length. The beans are seen to be very variable in form and coloring also.

from this mean are inversely proportional to their magnitude. The variation may be exhibited in size or number and the results of observation can be treated by mathematical signs and formulae.

GALTON, WELDON, BATESON, LUDWIG, DUNCKER, and many other investigators have raised this line of inquiry to a special branch of science. But, unfortunately, a recognized term for the phenomena with which they deal does not exist. It has been called fluctuating, gradual, continuous, reversible, limited, statistical and individual variability. The latter seems to be the most widely distributed in zoological and anthropological literature,

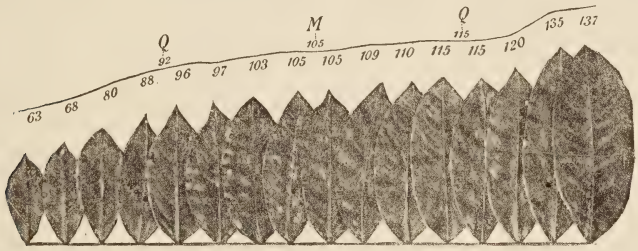


Fig. 11. The Ogive-form of the curve of individual variation, made of the leaves of *Prunus Lauro-Cerasus*.[1]

while the name fluctuating, which was often used by DARWIN, seems to be the best.[2] On the botanical side individual is opposed to partial variability, the former

[1] Individual variability can be very simply demonstrated by pasting the leaves of a tree in a row side by side. They are arranged according to their size and are placed at equal distances along a horizontal base line in such a way that their midribs are parallel; then their tips are joined by a line. In the above figure this line is placed at a little distance from the tips of the leaves for the sake of clearness. This line (the *Ogive* of GALTON, who has made most use of it) at first mounts quickly, then in the middle only slightly and at the end rapidly ascends again, following QUETELET's law. The points Q, M, Q divide it into 4 quarters (Q = Quartile).

[2] See KOLLMANN in Correspondenz-Blatt d. d. Gesellsch. f. Anthropologie, Bd. 31, No. 1, Jan. 1900.

meaning the differences between individuals, and the latter the equally frequent differences between the organs of a single individual.

The necessity of distinguishing between variability in space and time has been often insisted upon;[1] I mean between (a) the diversity in a group of forms existing at the same time, and (b) the differences existing between

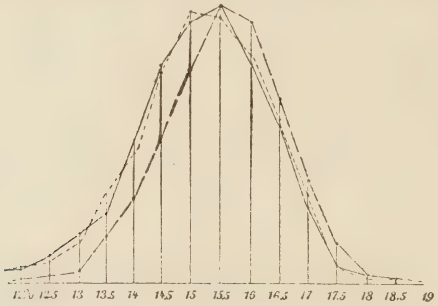


Fig. 12. Amount of Sugar in Beets, at Naarden.[2]
..... On January 24, 1896.
——— On January 25, 1896.
- - - - - On January 28, 1896.

parents and their children, and more distant descendants. Ploetz has proposed that contemporary varying indi-

[1] W. Waagen, *Die Formen des Ammonites subradiatus* in Benecke's Geognostisch-Paläontologische Beiträge, 1876, Bd. II, p. 186.

[2] The three curves exhibit the sugar contents of beets from one large sample taken from three successive determinations on January 24th, 25th and 28th, 1896, by exactly the same method. The numbers in each lot were 6848, 6781 and 6191, amounting almost to 20,000 polarizations. The sugar contents varied from about 12 to 19 per cent. These figures I owe to the generosity of Messrs. Kuhn & Co., the owners of the factories at Naarden.—In spite of the considerable number of values taken the curves do not exactly coincide. The third curve taken 3 days later has its apex shifted a little to the right. The differences between the 2 others are obviously to be attributed to unavoidable chance circumstances. In the comparison of empirical curves with theoretical ones, a closer agreement than that between 2 curves from 2 samples of the same kind must obviously not be expected. For theoretical purposes therefore one should, where possible, compare two or more curves of the same phenomenon.

viduals should be called Convariants, successive ones Devariants;[1] and individuals departing widely from the mean are often called variants.

Individual variability is exhibited by size, weight and number; LUDWIG's countings on flowers conform to QUETELET's laws as accurately as the anthropological measurements of that great writer himself. Variations in size and weight should be called quantitative, and BATESON has proposed for variation in numbers the name discontinuous or meristic.[2]

DARWIN asserted over and over again that this form of variability "perpetually occurs." It could therefore be described as perpetual or incessant, and this idea seems to me to be best expressed by the word continuous.[3]

Individual variability, when tested by sowing, reverts to its original mean, the forms of its variants are connected together, are coherent and not discontinuous. It is centripetal inasmuch as the variations are grouped most densely round a mean. Finally—and this is very important—it is linear; because the deviations occur in only two directions—less or more. This fact has given rise to the expressions plus-variations and minus-variations.

It is to the selection of the material afforded by individual variability that the origin of many improved

[1] ALFRED PLOETZ, *Die Tüchtigkeit unserer Rasse und der Schutz der Schwachen,* I, 1895, p. 31.

[2] *Materials for the Study of Variation.*

[3] I have used the terms continuous and discontinuous in this sense in my essay *Ueber halbe Galton-Curven als Zeichen discontinuirlicher Variation.* (*Berichte d. d. Bot. Ges.,* 1894, Bd. XII, Heft 7). BATESON uses the word in a slightly different sense inasmuch as he employs the term continuous solely for quantitative, and discontinuous for meristic variations (*Materials for the Study of Variation,* 1894).

races is due. But we must not forget, what we have already mentioned,[1] that the word "race" is used here in a different sense from that in which it is used in anthropology. The principal difference between the so-called im-

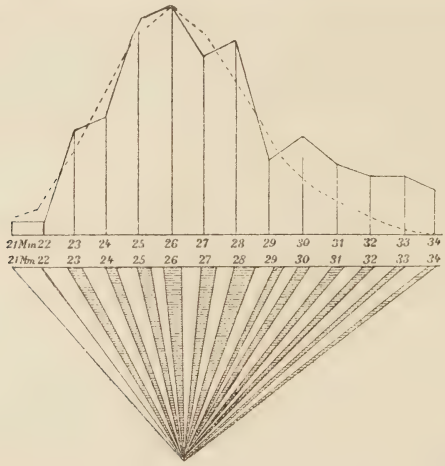


Fig. 13. Exhibition of Variability by the Fan Type of Plotting.[2]

proved races on the one hand, and varieties, subspecies, elementary species, incipient species and so forth, on the other, will form the subject of our third chapter.

[1] See page 41.

[2] Variability can be exhibited by other means than by QUETELET's curve (Fig. 10) or GALTON's Ogive (Fig. 11). If it is a question of comparing successive generations with one another the "fan" type of presentation (Fig. 13) is to be recommended. The point from which the rays emanate gives the character of the mother plant. The length of the base of each triangle on the upper horizontal line gives the length of the ordinates in an ordinary curve, as they are drawn above in the diagram. This breadth gives at a glance the frequency of individuals for any one scale character. The data for this figure consist of measurements of the length of the ripe fruits of *Oenothera Lamarckiana* taken in the year 1891 (99 fruits measured in whole millimeters). The lengths were distributed in the following way over the fruits:

mm.	21	22	23	24	25	26	27	28	29	30	31	32	33	34
	1	1	7	8	14	15	12	13	5	7	5	4	4	3

The crooked line follows QUETELET's law $(a+b)^n$.

4. *Spontaneous changes.* We have long been familiar in practical horticulture with the phenomenon of the sudden and unexpected appearance of varieties from time to time. DARWIN calls these sudden transitions *single variations.*

The finest examples are the so-called bud variations. The new form arises as a bud or twig on an individual of the old form and often remains a long time united with it. In a case like this there can be no doubt as to the mutual genetic relationship, and the fact that the transition is discontinuous is at once evident. But even in this sphere there is great uncertainty because bud variations are often born by hybrids and the hybrid nature of an individual is sometimes even betrayed only by such variations. Moreover bud variations are very common on varieties with incompletely fixed (mixed) characters, as in many forms with striped flowers (*Antirrhinum, Delphinium, Aquilegia, Dahlia,* Fig. 14, etc.)

5. *On the Magnitude of Mutations.* We often hear of spontaneous changes described as sports or as sport-like variations. This term is not a happy one. *Natura non facit saltus,* said LINNAEUS. But we are not told what we are to regard as a jump. There is much more point in describing the individual transitions as jerks and to speak of jerky variability.[1] The jerks may only induce quite small changes, but each jerk represents a distinct unit.

GALTON has illustrated the difference between jerking and ordinary variability in a very beautiful way. Imagine a polyhedron which can roll on a flat surface.[2] Every time that it comes to rest on a fresh side it takes

[1] *"Variation par secousses"* of some French writers.

[2] F. GALTON, *Hereditary Genius,* 1869, p. 369.

Fig. 14. Striped Dahlias (*Dahlia variabilis striata nana*), grown from seed. The central flower of the plant in the middle had yellowish red stripes on a pale red ground; the left flower on the same plant had one-half (shaded darker in the figure) entirely red, the other reddish yellow and pale red stripes. The two separate flowers figured below were of other color varieties; in the right one red stripes were on a white ground, in the left dark violet stripes on a pale violet ground. The first plant had branches, in 1898, whose flowers were entirely red, affording an example of so-called bud-variation.

up a new position of equilibrium. Little shocks make it totter; it oscillates round its position of equilibrium and finally returns to it. A slightly stronger push however can make it go so far that it comes to lie on a new side. The oscillations round a position of equilibrium are the fluctuations, the transitions from one position of equilibrium to another correspond to the mutations. The track left behind by the rolling polyhedron can be regarded as the line of descent of the species; each subdivision of this track, corresponding to a side of the polyhedron, representing a particular elementary species; each transitional movement to a new position a mutation.

The more numerous one imagines the sides of such a polyhedron to be, the smaller, of course, are the mutations. But this illustration gives no insight into the causes which effect the changes in position.

The observation of many single variations has introduced the view that mutations must always be considerable changes and especially that they should be greater than variations. But this is by no means the case, and it appears that many mutations are smaller than the differences between extreme variants. This is immediately clear if one compares e. g. *Draba verna* or *Typha angustifolia* and *latifolia*. The single species of *Draba verna* (discriminated by JORDAN, DE BARY, ROSEN and others), which have been shown by repeated sowing to be constant, differ less from each other than extreme variations in the same characters (form and size of the leaves, petals, pods, etc.) usually do in other plants; as can be seen best by comparing them with the partial variations of the leaves of our trees, that is, with the differences between the various leaves of one and the

same tree. And DAVENPORT and BLANKINSHIP have recently shown in a valuable paper that in the case of *Typha latifolia* and *angustifolia* the curves describing their various characters overlap. A small leaf of *latifolia* can be smaller than the broadest leaf of *angustifolia* and so forth. The curves overstep the limits between two species; they are transgressive and the species become "*intergrading groups.*"[1]

The differences between the single species of *Draba verna* (Fig. 3) afford one of the best examples for making clear, in a general way, the nature and size of mutations.

§ 5. THE ELEMENTS OF THE SPECIES.

Ever since DARWIN's theory of descent obtained general recognition, the need of an experimental study of the origin of species has always been strongly felt. This demand was always kept in the forefront by the few opponents of this theory, who objected that, so long as it was not possible to produce new species, or at least observe their origin directly, the foundation on which the theory rested was one of unproved hypothesis.

In the discussion of this objection two entirely different things are usually confounded. The origin of species is not the same thing as the origin of specific characters. The former is a historical occurrence; the latter is a physiological one. How, when and where species existing at the present moment arose is a subject for historical investigation, and we can only discover anything definite about it in those rare cases in which records have been kept by contemporary eye-witnesses. The problem of

[1] C. B. DAVENPORT and J. W. BLANKINSHIP, *A Precise Criterion of Species; Science*, N. S., Vol. II, No. 177, p. 685, 1808.

accurately tracing the formation of a given species is certainly a most attractive one; but its solution falls within the province of comparative biology.

The origin of specific characters is a matter for physiological investigation, and is of the very highest importance. We hardly know what specific characters are. We know, it is true, that elementary species and forms closely allied to them, are distinguished from one another not by a single feature but by all their organs and peculiarities.[1] The differences between two closely allied forms often demand a long and extensive diagnosis. Nevertheless this diagnosis must be regarded as the expression of a single character, a single unit, which arose as such and as such can be lost; the individual factors of which cannot be manifested separately. Theoretically such a group of characters must be regarded as a unit, as a single character.[2] It forms a single side of GALTON's polyhedron (p. 53). DARWIN called such characters the elements of the species and consequently we may call each of the forms distinguished by such an element, an elementary species.

How these elements of the species arise must sooner or later become the subject of experimental investigation. If we once succeed in solving this question we shall obtain not only a much surer foundation for the theory of descent but the prospect of the utilization of this discovery for the benefit of mankind. The only means by which the breeder can get new forms is by hybridization, and all that he can do by selection is to intensify the produce and yield of characters already present; but

[1] This fact forms a hitherto little noticed support for the theory of homotypic cell-divisions as advanced by HERTWIG and others and by myself in my *Intracellulare Pangenesis* (See e. g. p. 115).

[2] *Intracellulare Pangenesis*, p. 16.

so far it is not within his power to call into existence new characters. We all know that it is said to be impossible to produce a blue Dahlia, a bright yellow Hyacinth and so forth. To give our large flowered Canna white flowers we must wait for the discovery of a new white flowered wild species and then cross it with it (Crozy); in the same way that our Gladioli have been made hardy and the flowers of our Begonias large by crossing them with newly discovered species which possess the character in question. As soon as we arrive at an experimental physiology of the origin of species, we expect to obtain control over much that at present seems beyond our reach.

But let us return to the facts. Whilst we may hope that the origin of new elementary species will one day become the subject of direct investigation, we must be perfectly clear as to the essential difference between these and the so-called Linnean species which are (usually) groups of elementary species. An elementary species can be identified in any given case by the test of cultivation; how many such forms should be united to one Linnean species is a matter for so-called taxonomic instinct, just as is the settlement of the limits of genera and families.

Let us return to the rolling polyhedron and look at the track it has left behind. Each piece of it, formed by one side, represents an elementary species, and we will imagine that all such species of a certain strip of the path have left living offspring. The question is where to place the boundaries of a "species" in such a group.

Instead of a discussion I shall give the answer which one of the most famous of the older systematists, Hooker, has given in certain definite cases. First in regard to *Oxalis corniculata*. The forms of this collective species,

which grow in New Zealand, have been raised by CUNNINGHAM into 7 well-defined species; but since connecting links between all these seven forms are found in different countries HOOKER has united them into a single species.[1]

Another good example is furnished by *Lomaria procera,* a fern from New Zealand, Australia, South Africa and South America. If we were acquainted with the forms from one of these localities only, we should recognize, in them, a number of species. But when those from all these localities are compared they form a complete series, and they are consequently united as a single species. But this species comprises a much larger series of forms than all the remaining species of Lomaria put together.

The limits of collective species arise therefore by the dropping out of links in the chain of elementary species. These gaps are apparent when one confines his attention to a single region; and real if they still persist when the Floras of the world have been examined. If the *Oxalis corniculata* or the *Lomaria procera* ceased to exist in any one country the present species would have to be split up into smaller ones.

Or in other words: Linnean species arise by the disappearance of single elementary species from a hitherto unbroken series. This origin is therefore a purely historical occurrence and can never become the object of experimental investigation.[2]

"Species" therefore have very little physiological sig-

[1] J. D. HOOKER, *Introductory Essay to the Flora of New Zealand,* 1853, p. 18. Compare also HOOKER's account of *Aconitum Napellus.*

[2] The famous expression of SPENCER, *The survival of the fittest,* is therefore incomplete and should run *the survival of the fittest species.*

nificance, whereas the study of specific characters will some day form the most important branch of investigation in the whole domain of biology.

Fig. 15. *Zea Mays tunicata* (or *cryptosperma*). Three ears from a sowing of seeds from the same ear. The individual seeds are enclosed in the husks; in A however, incompletely covered about the middle of the ear, and almost naked at the top. C is the intermediate form; B has, especially below, very large husks.

Continuous Variation of Elementary Specific Characters.—The difference between fluctuation and mutation perhaps comes out most clearly in this connection. By

mutation new characters arise all at once. Such characters are however just as variable, and vary in the same way as those specific characters with which we are already familiar.[1] There are so many examples of this rule that it is difficult to make a choice.[2] *Zea Mays tunicata* or *cryptosperma* has its seeds enveloped in husks, but the length of these husks varies in a high degree; sometimes they scarcely cover the seed, in other ears they are

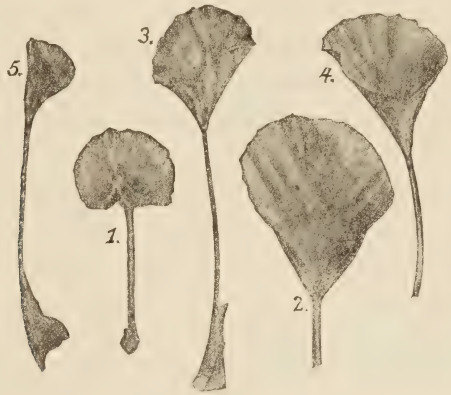


Fig. 16. Leaves of *Saxifraga crassifolia* in various degrees of pitcher formation, the succeeding stages being represented by the figures 1-5. This process can be imagined as consisting in the edges of the leaves folding upwards and fusing together. The degree of this fusion is seen to be very variable.

3 or 4 times as long, if not more. Very often they are much longer in the lower part of one and the same ear, than in the upper; and their length gradually decreases as the apex of the ear is approached (Fig. 15). Variegated leaves, double flowers, pitchers (Fig. 16), split leaves and so forth occur in great variety, and it would not be difficult to demonstrate the applicability of Que-

[1] See also *Intracellulare Pangenesis,* pp. 69-70.

[2] For examples from the animal kingdom see Bateson, *Materials,* p. 68.

TELET's laws to these cases. For each character there is a mean, around which the variants are grouped according to the laws of probability. In similar fashion, the splitting of the leaves in *Chelidonium laciniatum,* varies; even glabrous and unarmed varieties exhibit a certain degree of variability in the extent to which they manifest the character which they are supposed not to possess. (Young shoots of *Biscutella laevigata glabra,* fruits of *Aesculus Hippocastanum inermis,* and so forth.) Five leaved clover (*Trifolium pratense quinquefolium*) varies in the number of leaflets between 3 and 7, obviously following QUETELET's laws.[1] The characters peculiar to *Papaver somniferum polycephalum* (Figs. 27 and 28, Chap. IV, § 16) and *Papaver bracteatum monopetalum* (Fig. 1, p. 12) are in the highest degree variable. The same is true of the syncotylous and tricotylous races. The widest range of variability and complete immutability are frequently associated.[2] Such variation or fluctuation is therefore an occurrence of quite a different order from mutation.

§ 6. THE MUTATION HYPOTHESIS.

Although I do not intend to discuss the views of my contemporaries on selection and mutation at large in this work,[3] I shall now call attention to the fact that objections are continually being raised against the theory of selection from all sides.[4] The authors in question

[1] *Over het omkeeren van halve Galton-curven, Botanisch Jaarboek of the Society Dodonaea,* X. Jahrg., 1878, p. 46.

[2] *Alimentation et Sélection. Vol. Jubilaire de la Société de Biologie de Paris,* Dec. 1899.

[3] For a critical presentation of both sides of the question the reader is referred to O. HERTWIG, *Zeit- und Streitfragen der Biologie.*

[4] See also BATESON, *Materials,* p. 567.

express themselves more or less definitely in favor of the mutation hypothesis.

E. D. Cope was the first to clearly formulate objections against the doctrine of selection. Selection preserves the good and weeds out the bad, but whence does the good arise? Obviously ordinary variability is not sufficient, and causes of an entirely different kind must be sought for. Such causes he includes under the term bathmism.

Carl Semper similarly rejects the selection theory and ascribes considerable importance to the influence of the environment, the so-called *monde ambiant* of the French school, in originating useful specific characters.

Louis Dollo was the first to express the view that *l'évolution est discontinue* from the standpoint of the theory of descent. He supports his statement by a series of facts, partly zoological, partly botanical, but especially derived from his own researches in paleontology. He puts forth the additional proposition that *l'évolution est irréversible et limitée.*[1]

According to Wallace's selection theory, progressive change by artificial and natural selection is supposed to be unlimited and even reversible. It must be reversed according to Wallace as soon as the conditions on which the selection depends are themselves reversed. According to the mutation theory, on the other hand, no cause can be assigned which would make a mutation reversible, apart from the loss or latency of characters. Each mutation is a definitely circumscribed unit.

About a year later there appeared Bateson's famous work *Materials for the Study of Variation Treated*

[1] Louis Dollo, *Les Lois de l'évolution. Bull. Soc. Belge de Géologie,* T. VII, p. 164, Année 1893.

Especially with Regard to Discontinuity in the Origin of Species. The special part of this book consists of an exhaustive catalogue of instances of variations in number, or so-called meristic variations, in the animal kingdom. Variations and mutations in the number of vertebrae, of fingers, of joints of the tarsus, etc., are set forth, and are included under the term discontinuous variations.[1] The general part is devoted to a critique of the modern theory of evolution. The theory of descent has, according to BATESON, not merely to account for the kinship of organisms. This point is already granted. But it also has to explain the differences between individual forms and, with regard to this point, BATESON asserts with perfect right that the species alive at the present day are sharply and completely separated from one another, and that transitions between them either do not occur at all, or at most, very seldom. Existing species form a discontinuous series. The theory of descent, therefore, has to account not only for their relationship, but also for this discontinuity.[2] The latter forms one of the weak points in the current theory of selection. For according to this theory, the series of ancestors of any given organism must be a continuous one, seeing that the only differences between parents and offspring are of the so-called individual or fluctuating kind. Whence then arise the gaps which now separate species from their nearest allies?

The usual answer that is given is to point to the existence of numerous intermediate forms These however are not transitional forms, but independent types, namely

[1] See especially pp. 568 and 571; also pp. 15, 61, etc. The argument of DUNCKER (*Biol. Centralblatt*, 1899, p. 373) is therefore not really directed against BATESON'S use of the term *discontinuous*.

[2] See pp. 5, 17, etc.

elementary species or subspecies. BATESON expressly points out that the law of elementary species holds good for the animal as well as for the vegetable kingdom; but that these forms have as yet received much too little attention. Elementary species are sharply and completely separated from one another, they do not merge into one another, either in the wild state, or under cultivation (provided that crossing does not occur).

This sharp delimitation of the elementary species is so general a phenomenon that it certainly points to a discontinuous origin. The main object of BATESON'S book is to arrange and collect the material in such a way as to give some insight into this discontinuity.[1]

A very serious objection to the theory of selection is brought forward by him in reference to the usefulness of specific characters.[2] It has been repeatedly asserted by DARWIN and others that the characters which separate allied species from one another are not of particular advantage in the struggle for existence, but are as a rule useless and inconsiderable. Nevertheless these differences are often, apparently, very complex and constant characters but "of doubtful value." The existence of such characters cannot be accounted for by WALLACE'S theory of selection which explains useful characters in so beautiful and simple a manner. The mutation theory, on the other hand, gives a perfectly simple explanation of the existence of such characters; for useless, but not dangerous, mutations must appear as often as useful ones, and have almost as much likelihood as these of persisting.

[1] Species are discontinuous; may not the variation by which species are produced, be discontinuous too? p. 18. See also pp. 69, 568.

[2] Page 11.

BATESON's conclusion is expressed in the following words: *The evidence of variation suggests in brief, that the discontinuity of species results from the discontinuity of variation.*[1]

W. B. SCOTT, in an exhaustive critique, has expressed his opposition to many of the views in BATESON's book.[2] He particularly objects to the statement that species form a discontinuous series. He adduces recent paleontological discoveries as proof that there are no such gaps in the genealogical trees of the horses or of many other mammals. Such series are only discontinuous when our knowledge concerning them is incomplete. In continuous series the progression took place *by almost imperceptible gradations.*[3] These gradations seem, however, to be what BATESON calls steps. Let us return to the simile of GALTON's rolling polyhedron. The question whether we choose to call this movement continuous or discontinuous depends on our point of view. Even a series of numbers can be unbroken and therefore continuous.

The word mutation has been used more in paleontology than in other sciences to express the differences between allied species. The actual process of mutation, the change of one species into another, can obviously not form a problem of paleontology. The paleontologist can only study the series of consecutive forms. From such series however important information may be derived as to the size of individual steps, that is to say, the mutations. WAAGEN has said that the more complete the geological evidence is the less perceptible do

[1] *Loc. cit.*, p. 568.

[2] W. B. SCOTT, *On Variations and Mutations.* Am. Journ. Sci., 8° series, vol. 48, Nov. 1894, pp. 355-374.

[3] Page 360.

the specific gradations become.[1] We can obviously never know how much more numerous, if at all, the mutations have been than the species whose remains we find; countless species may have arisen without leaving a trace behind, but whether this is the result of the struggle for existence, of natural selection, or of an advance in a predetermined direction, cannot now be ascertained. Phylogenetic changes make straight for the goal, seldom swerving to the side, hardly ever advancing in a zigzag line,[2] but whether natural selection or variation in a definite direction was the determining cause is obviously a matter of personal opinion.

The constancy of forms arising by mutation, as opposed to fluctuating variability, is supported by the results of paleontological research. WAAGEN as well as SCOTT and others have declared against WALLACE'S selection theory on these grounds. They strongly maintain that mutations must be admitted to a more prominent place in any theory of evolution.[3] Each "mutation" (elementary species) serves as a new center of analogous variations.

SCOTT deduces from paleontological data a further series of conclusions relative to the occurrence of mutations. I find many of these views supported by a critical study of the theory of variation as well as by my own experimental work. I shall have to return to them at the conclusion of this section, and in the first chapter of the following one.

Last year KORSCHINSKY definitely expressed himself as opposed to the present form of the selection theory.

[1] WAAGEN, *Benecke's Geogr. Paläontol. Beiträge,* II, S. 170.

[2] SCOTT, *loc. cit.,* p. 370.

[3] *Loc. cit.,* pp. 372, 373.

He includes mutations or spontaneous variations under the term heterogenesis on the analogy of KÖLLIKER's heterogenetic reproduction and the "Heterogenism" of HARTMANN.[1] He bases his conclusions on the data of horticultural practice and gives a complete and very important survey of the cases in which the history of the first appearance of varieties is more or less accurately known, or in which the occurrence of new forms other than by a series of transitional stages points to a sudden origin.

Such heterogenetic changes (the mutations of the older investigators) can be progressive or retrogressive, that is the organs can become more complicated or more simple; both kinds of changes must often happen, but the retrogressive ones can obviously occur more easily than progressive ones. Mutations can be induced, as DARWIN also believes, by the cumulative operation of favorable conditions during development and by rich nutrition continued through many generations. Forms that have newly arisen can sometimes be so sharply distinguished from the parent type that any systematist would take them for a separate species if he did not know their origin.

KORSCHINSKY concludes from a survey of the facts at his disposal that among garden plants all new forms, or more strictly all new characters, have originated by heterogenesis. New varieties are not obtained in horticulture by the selection or cumulation of individual differences. Selection is a conservative agency. It fixes new

[1] S. KORSCHINSKY, *Heterogenesis und Evolution, Naturwissenschaftliche Wochenschrift,* 1899, Vol. XIV, No. 24. A larger work appeared in the *Memoires of the St. Petersburg Academy of Sciences,* 1899, Vol. IX. See also *Flora,* Vol. 59, 1901, pp. 240-363. (Note of 1908).

characters that have already arisen but it cannot of itself produce new forms.

This author then proceeds to a comparison of the fundamental principles of the selection and mutation theory. As a result, he finds that the theory that species have originated by the selection of individual differences is beset with series difficulties, whereas the belief that this has taken place by mutations (heterogenetic variations) provides us with a satisfactory explanation or at any rate is in close accord with the facts. Two facts that strongly favor this view are (1) the absence of transitional forms and (2) the existence of at least apparently useless characters.

DARWIN's view is that the probability of a progressive development in animals and plants is great in proportion to the severity of the struggle for existence. KORSCHINSKY on the other hand holds that favorable conditions afford the best opportunity for the appearance of mutations. For the new forms in order to establish themselves require suitable opportunity for the development of their powers and fertility to the full. It will be seen that this contrasts strongly with DARWIN's view, which is that the innumerable weaker variants simply cease to exist while the rarer stronger ones survive.

I shall now close this historical sketch. I hope, at a later date to review more fully the views of modern authors; it will then be seen that the general opinion is that the theory of selection is unsatisfactory. For example DUNCKER says that individual variability is static rather than kinetic; and therefore does not provide material for natural selection.[1] Lord SALISBURY said in his presidential address at the meeting of the British

[1] *Biolog. Centralblatt,* 1899, p. 373.

Association in Oxford in 1894:[1] The theory of selection is by no means to be regarded as proven; for a host of difficulties stand in the way of the acceptance of the explanation of evolution by the accumulation of ordinary (individual) variations. And still more recently Rosa,[2] from the standpoint of critical studies in phylogeny has insisted on the distinction between mutations and fluctuations, considering only the first group as phylogenetic variations.

[1] *Nature,* Aug. 9, 1894.

[2] D. Rosa, *La riduzione progressiva della variabilita e i suoi rapporti coll'estinzione et coll'origine delle specie,* Torino, C. Clausen, 1899, p. 93.

III. SELECTION ALONE DOES NOT LEAD TO THE ORIGIN OF NEW SPECIES.

§ 7. SELECTION IN AGRICULTURE AND HORTICULTURE.

Botanical literature affords very few instances of scientific experiments on artificial selection. And so long as this continues to be the case we shall be thrown back on the experience of breeders.

One of the best scientific experiments of this kind is FRITZ MUELLER'S on Selection in Maize.[1] He dealt with the number of rows on the ears (Fig. 17) and started by choosing the ears with the greatest number of rows for sowing; the commonest were those with 10-12 rows; the others group themselves round this figure in familiar fashion according to QUETELET'S laws. Among many thousands of ears a single one was found with 18, but none with 20 rows. At the end of three years selection the mean had shifted to 16 rows, while single ears had as many as 26 rows.

I have repeated this experiment over a longer series of years, and have exhibited the result in the form of a genealogical tree, plotting the variability by the fan method as explained in Fig. 13, p. 52. The fans have been reduced by substituting the most essential lines for the numerous triangles of Fig. 13. The middle line of each

[1] *Kosmos*, 1886, Vol. II, p. 22.

fan corresponds to the mean (the apex of the curve), the two dotted lines to the quartiles Q and Q_1; between which therefore lie that half of all the individuals coming nearest to the average. The two outer lines of each fan denote the ears with the greatest and smallest observed number of rows; their divergence is of course largely

Fig. 17. *Zea Mays.* Ears with 8, 16 and 22 rows of seeds from my experiment in selection carried out from 1886-1894.

dependent on the size of the harvest; this amounted on the average to about 200 ears a year.

Of the two lines going from top to bottom the right-hand one represents the numbers of rows on the ears actually chosen for sowing. That is to say there were sown seeds from ears with 16 (1887), 20, 20, 24, 22, 22, and 22 rows; ears with a greater number of rows

were usually too poor in seeds to be of any use for continuing the experiment.

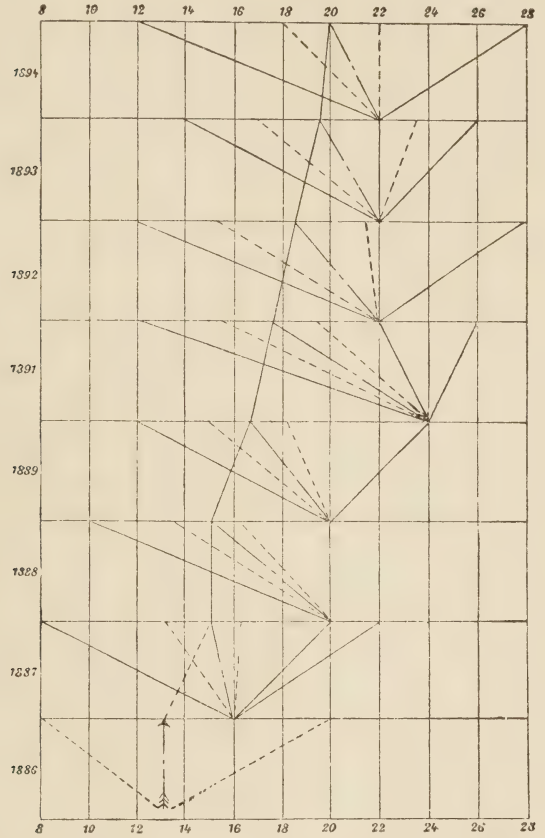


Fig. 18. Pedigree of an Experiment in Selection with Maize. The numbers at the top and bottom of the figure show the number of rows in the ear. The experiment began in 1887; the lines for 1886 give the characters of the race with which I started.

The left-hand line joins the ends of the middle rays, which correspond to the apices of the curves for each

year. It shows us therefore the mean progress of the yield. This line comes closer every year to that of the ears used for seed. A proper study of its course would have necessitated the undertaking of effecting artificial self-fertilization which in the case of maize is known often to lead to a poor harvest. I should have preferred to have used another plant, had not the ears of maize lent themselves so admirably to a demonstration of this kind.

It is not necessary to repeat that the experience of breeders provided the main support for DARWIN's selection theory. In its broad outlines the process of natural selection is like that of artificial selection. But as soon as we come to dissect the component factors of these processes we encounter serious difficulties, as I have already remarked in the Introduction.

The chief cause of this state of affairs is to be sought in the circumstance that breeders rarely work with single characters but have as a rule aimed at improving their plants in every possible respect,

They never attempt a separation, or even a separate observation, of special characters. The second cause is that breeders have no interest in distinguishing between their different methods of improving their plants. On the contrary it is usually the best plan to allow the various methods: of the choice of desirable mutations, of their gradual improvement by repeated selection, of natural or artificial crossing, of manuring and what not, to exert their combined effect.

The breeder is only interested in the result. The means by which this has been attained is a secondary matter and is seldom thought worthy of an accurate record.

In choosing cases for the scientific study of the process of selection it is of the highest importance to exclude all those in which crossing has taken place, or where it has not been excluded with absolute certainty. Many genera and species owe their present range of forms (which is what breeders call variability) almost entirely to the repeated crossings between the original wild forms that were introduced, whether these were different Linnean species or numerous elementary species of such.

There are two chief categories to be distinguished. First there are those genera in which a very wide range of form is desired, and for this purpose almost every conceivable cross between the different varieties has been carried out. The best, either from the utilitarian or from the decorative point of view, are then put on the market and are, in the eyes of the layman, an inscrutable medley. Fuchsias, dahlias, chrysanthemums, wheat and potatoes are the best known examples. The novelties of the breeders arise in these cases almost without exception by the deliberate combination of characters already existing in the old types.

Secondly there are the genera which have developed in a definite direction since the beginning of their cultivation, e. g., begonia, gladiolus, caladium, amaryllis, canna and many others. The improvement in these cases has almost always been the result of the discovery of new wild species. These have been crossed with the cultivated bastard race and in this way the desired characters of the former have been transferred to the latter. The large and beautiful blossoms, the caladiums with variegated leaves, the hardy gladioli etc. have been got in this way. The characters of the new varieties already existed in nature, distributed between the different spe-

cies. The combinations are new in cultivation; but the characters themselves do not owe their origin to it.

Of course I do not deny the appearance of mutations in cultivation, but so far as I have been able to learn personally from the best known breeders these are relatively rare occurrences.

It is impossible to insist too much that the much talked of progress in cultivation is a delusion if the part played by crossing is left out of account or if the results of this crossing are regarded as the effect of selection. And this happens only too often. Hybridization is so much more certain and easy a way than selection of getting something new that breeders would nearly always be working against their own interests if they did not expose their plants as freely as possible to natural cross-fertilization. The possibility of crossing should evidently only be excluded when we are concerned with the fixation of races or with methodical selection carried out according to strict principles. *But it is only experiments of this kind that have any value for the theory of selection.* Unfortunately they are much more rarely carried out, or at least more rarely described than one could wish.

Most of the brief notes made by breeders on variability, which is apparently considerable, are open to the objection that the seeds in question have been collected from plants fertilized by the wind or by insects. And if, for example, we read through the mass of material collected by DARWIN, with this in mind, we shall find that much that seemed to be variability or mutability receives a much simpler explanation by supposing that it was the result of crossing or of the collection of seeds from hybrid plants. It will always be found that the number

of cases of alleged variability in plants whether in the wild or cultivated state suffers a considerable shrinkage so soon as one views the individual statements from the point of view of possible chance crossings.[1]

I maintain, in a word, that much that has up to now been alleged as evidence of variability overstepping the limits of elementary species (that is mutability) should really be attributed to the result of unobserved chance crossings.[2]

It is worth while to draw attention to the further distinction between agricultural and horticultural selection. For a clear perception of the relations existing between them will facilitate our understanding of the difference between fluctuations and mutations.

Every year there are put on to the market by professional gardeners a certain number of so-called novelties especially of plants propagated by seeds, for it is these that I have particularly in view.[3] They are partly hybrids, partly really new varieties and subspecies, partly species brought from foreign lands. The varieties and subspecies arise suddenly and only a few individuals of them occur as a rule. They seldom appear in the nursery gardens but usually in those of customers, whose total area is of course much greater than that of the firms which supply the seeds, and where as a rule much more time and attention is devoted to the individual plants.

[1] See also HOFFMANN, *Botanische Zeitung*, 1881, p. 381. "The seeds of isolated flowering examples have shown no tendency to the formation of variations."

[2] In a later section I propose to deal with this comparison exhaustively and from the point of view of careful experiment.

[3] The commercial aspect of breeding has been most thoroughly gone into by C. FRUWIRTH, *Züchtungsbestrebungen in den Vereinigten Staaten*, in FÜHLING'S *Landwirthsch. Zeitung*, 1887, Jahrg. 36, p. 16.

The nurserymen then usually buy the novelties from the customers in question at a considerable price. As a rule 4 or 5 years elapse before such a novelty is put on the market. During this time, so we are told, it has been made constant by selection. It would be more correct to say that they are freed from the adulterating effects of free crossing. For the selection consists in weeding out the so-called rogues at the time of flowering (supposing that we are dealing with flowering plants) in order to save seed only from the pure individuals. But if we are dealing with vegetables the selection takes place long before they are in flower, so that there is no danger of crossing in this case.

These rogues are nothing more than hybrids resulting from free crossing in the preceding summer. I have often had the opportunity of watching this weeding out. It takes place at the height of the flowering season. The pure individuals may therefore have been already partly fertilized by the rogues; and for this reason some of the seed for the next year may have been contaminated. The sole object of the selection is to reduce the mixture with other forms to a minimum; the pollination is left to insects from the first generation onwards, so that cross-fertilization always takes place. I have never been able to find that in ordinary cases selection had any other object than the purification of the new race from the effects of mixed ancestry.

The use the gardener makes of his 4 or 5 years is to increase his stock of seed sufficiently to make it worth while to put it on the market. This is in fact a far more important matter than the process of purification that we have been speaking of. As soon as the requisite quantum of seed is obtained it is put on the market. Absolute

purity is not guaranteed. I have often bought seeds of novelties and tested their purity by extensive sowings. They almost always contain impurities. But whenever I fertilized some specimens of the new forms with their own pollen after taking care that the visits of insects were excluded, they came absolutely true in the next generation. We all know that we are lucky if we get a purity of 97-99% ; the remaining 1-3% are, we are told, atavists; as a matter of fact they are practically always the survivors of the impurities that owed their origin to free crossing in the field.

The whole profit on a novelty must be made during the first year of its appearance in the trade.[1] For as soon as it bears seed in other gardens its originator loses the monopoly of it. For this reason novelties are usually offered for sale towards the end of the year in special price lists to as many seedmen as possible; they introduce them into their catalogues, and that is why one usually finds that most novelties are put on the market simultaneously by numerous firms. Their price is at first considerable, but in a few years sinks to the normal, for by that time as much seed as wanted can be produced everywhere.

A horticultural novelty, when it has once arisen and has been freed from the results of crossing and put in sufficient quantity on the market, is everybody's plant. All that remains to be done to keep them constant is to avoid foreign pollen.

The case of agricultural varieties, on the other hand, is quite different. I am referring now only to the genuine improved races and give the description of their pro-

[1] I have often heard the value of such a novelty set at £100 to £150.

duction according to the now current views.[1] They do not arise by chance, they are not the result of rare and sudden variations. The material out of which they are made is furnished by fluctuating variability. At the outset, the breeder seeks in his fields for those plants which seem the best for his purpose, and collects their seeds separately. These plants differ very little in the eyes of a layman from the other specimens in the field. He sows seeds from these on a small scale, working every year on the same principles, in this way gradually increasing the deviations from the original form in the desired direction.

He has as a rule one or two qualities chiefly in view, but pays attention where possible to all other characters. He is not concerned with the improvement of one particular quality. To achieve this many things are necessary, patience, an intimate acquaintance with the species of plants in question, and a firm and clear conception of the ideal to which he wishes his race to attain. And in spite of the possession of these qualifications the best known breeders are by no means successful with every experiment; the greatest of them, that is those who have introduced the most widely distributed races, have often only brought out one or at most a very few successful novelties.

The value of such a race gradually increases. At first as seed for one's own purpose, but soon as seed for the market. But the seed is not put on the market in a single year but gradually during the period of improvement and multiplication. The improved characters de-

[1] For the earlier constant products of selection, e. g., those of Patrick Shirreff, and for my own views concerning the description given in the text see the conclusion of § 12, pp. 109 ff. and § 23, pp. 178 ff. (Note of 1908.)

teriorate as soon as the new race is cultivated on a large scale, on account of the consequent cessation of rigid selection. The harvest has therefore less value than the original sample of seed. In this way the breeder is assured the monopoly of his prize for many years until, may be, his race is superseded by another and a better one.

The work done and the profits made by the horticulturist are insignificant compared with those of the agriculturist. The former introduces a few novelties into the garden every year. The latter increases the yield of whole countries. I have often heard farmers speak with pride of their results as compared with those of gardeners.

Finally I would mention a good example of the difference in question. BESELER in Anderbeck by years of patient work improved his oats to such an extent that he was able to put them on the market under the name of Anderbecker Oats. This form was bearded, a feature which was found fault with from many quarters, and prejudiced its sale. It was a small matter to make Anderbecker Oats beardless, provided that beardless examples could be found. This happened to be the case; and since that time BESELER'S oats have been beardless.[1]

This difference between the practice of agricultural and horticultural breeding has in my opinion been largely responsible for the present form of the scientific theory of selection. That which can only be achieved by a few and at the cost of great sagacity and patience, produces a great impression; that which chance can put into the hands of any one, makes none at all. And so it comes about that the former method has loomed much larger

[1] v. RÜMKER, *Getreidezüchtung*, 1889, pp. 60, 75, and 94

in our discussions on the origin of species, whilst the latter has been relatively neglected. But it must not be forgotten that the agricultural improved races do not possess the constancy of true species;[1] whereas the varieties and subspecies of the horticulturist can only be distinguished from true species historically and systematically—not experimentally.

In conclusion: we see that in estimating the value of the experience of breeders for scientific purposes we have to fix our attention on the simplest processes. Everything that can be considered the direct or indirect result of crossing must be excluded before we consider its bearing on the theory of mutation or selection. Furthermore one must sharply distinguish between the races that have been produced by continued selection, and the constant forms which owe their origin to a sudden fortuitous change.

In horticulture varieties arise by mutations, and varieties are elementary species. In agriculture according to the current view and excepting in the instances of the unconscious isolation of elementary species, the highly improved races arise gradually through selection, but they never become species.

§ 8. SELECTIVE BREEDING FOLLOWED BY VEGETATIVE PROPAGATION.

We shall now proceed to deal with the scientific significance of selection in those cases in which its products are multiplied vegetatively.

[1] Or if they do prove to be constant, they usually turn out to be the result of the unconscious isolation of elementary species; compare Nilsson's results, described in § 12, pp. 114 ff and *Archiv für Rassenbiologie,* April 1, 1906. (Note of 1908.)

Properly speaking these cases have no significance for the theory of descent. But they are so much more striking than the results of selection in seedplants that they are often used as examples.

If after extensive sowing, or after repeated selection of any species one gets a single example with large flowers or fruits or with any desirable character in an exaggerated degree there are two possibilities.

First one may be dealing with a seedplant, that is with a species which can either be propagated only by seed, or in which it is usual to propagate it in this way in practice.

Secondly, one may be dealing with a plant which is capable of vegetative propagation whether by division of the rhizom, by cuttings, by grafting, by tubers, or by any of the other ways in which this may be effected.

In the first case the seeds conform to the law of regression. This was recognized by VILMORIN and afterwards scientifically studied by GALTON. If we regard GALTON's formula as generally true the mean of the offspring deviates from the mean of the type in such a way that it retains only a third of the deviation of the parent. So that to produce a given advance in the whole family we should have to sow seed from a plant which had advanced three times as far.

To make the meaning of this regression clear I will select as an example a culture of *Madia elegans*. The mean number of ray-florets on a flower head is 21, and the other numbers are grouped round this in accordance with QUETELET's law. In the 1892 crop of my experiment the mean was 21 and the variation lay between 16-25; of these I chose 6 examples, each possessing 16-19 rays in the terminal head. From their seeds I obtained

a series in 1893 varying between 12 and 22 and with a mean of 19 rays. I now chose the seed from 13-rayed plants and got in 1894 a generation varying between 13 and 22 and with a mean of 18. The regression amounted in this experiment to about ⅓; that is to say the children deviated only one-third as much from the type of their species as their parents did.[1]

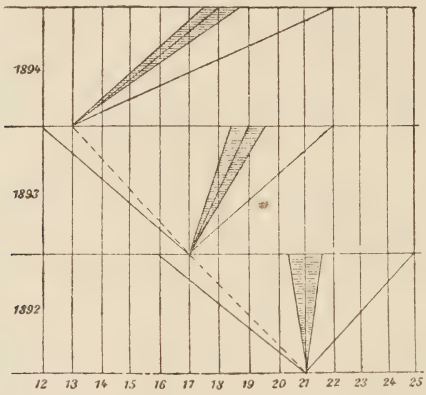


Fig. 19. *Madia elegans.* Successive generations showing the result of the selection of examples with the smallest number of ray-florets. The figures at the base of the ordinates give the number of these florets. The limit of the variation fan for 1904 coincides on the left side with the 13 rays ordinate.

On the other hand a character perpetuates itself unaltered or almost so if the plant bearing it is propagated vegetatively. The descendants are of course nothing more than parts of the original plant; the products of a single seed. Hundreds or even thousands of them can be put on the market, but together they constitute merely parts of a single individual.

The whole so-called variety, thus, consists in this

[1] See also the pedigree of my experiment with maize on p. 73.

case of a single individual. This is true in the case of apples and pears and many other fruit trees; of tulips and other bulbs, of dahlias, canna and so forth. Among agricultural plants it is true of potatoes, among plants from tropical countries, of bananas and of sugar cane and so forth.

Strictly speaking a variety of this kind cannot be compared with that of a plant propagated by seed. It is, on the contrary, analogous to the single plants chosen to furnish seed for market stock. If we assume GALTON's formula to be applicable to this case also we may say that the results of selection are three times as great when the plants are propagated vegetatively as when they are propagated by seed.

So that, if we adduce the splendid flowers of our bulbs, the size of our potatoes and the excellence of our fruit as examples of a high degree of variability and of the perfection that can be attained by selection we must never forget that, in the light of what we now know on this head, the improvement would have to be diminished by ⅔ if the results were to be applied to the theory of descent. And if we do make this reservation nothing much is left, from the biological standpoint at any rate.

§ 9. ON THE DURATION OF THE PROCESS OF SELECTION.

The modern theory of selection rests on two unproved hypotheses:

1. The advance brought about by selection may increase for an indefinite period.

2. The result of selection can become independent of selection.

The experience of breeders stands in direct contradiction to both these hypotheses.

Let us examine these statements separately. We may consider the first under two headings according as the period in question refers to the future or to the past; that is whether we are concerned with explaining a form already existing, or with predicting its possible changes.

Let us begin with the past. *These changes have been the result of some 1000 years of domestication and selection,* says WALLACE.[1] And DARWIN said, as a result of a criticism of HOFFMANN, *"Perhaps hundreds of generations of exposure are necessary."*[2] And in another place, *"I cannot doubt that during millions of generations individuals of a species will be born with some slight variation profitable to some part of its economy."*[3] Again ALPHONSE DE CANDOLLE, speaking of acclimatization, says in a similar strain: "Il faut, parait-il, pour une modification permettant de supporter des degrés plus intenses de froid, des périodes beaucoup plus longues que 4 ou 5000 ans, ou des changements de forme et de durée."[4] Of more modern authors J. COSTANTIN writes as follows: "Mais si pendant 50, 100, 1000 ans l'action du milieu se maintient toujours la même, les caractères héréditaires qui évoluent lentement, se consolident, deviennent de plus en plus stables.[5]

Numbers of similar passages will doubtless occur to the reader, but if he examines them carefully he will see that whilst, to DARWIN, the long period of time meant

[1] WALLACE, *Darwinism,* 2d ed., p. 89.

[2] *Life and Letters,* III, p. 345.

[3] *Ibid.,* II, p. 124.

[4] *Origine des plantes cultivées,* p. 371.

[5] COSTANTIN, *Accomodation des plantes aux climats froid et chaud. Bull. Scientif.* de GIARD, T. 31, 1897, p. 489.

nothing more than the likelihood of the chance origin of a useful change, to WALLACE on the other hand it meant the operation of time by the gradual cumulation of fluctuating variations in the same direction. Other authors sometimes mean one of these things, sometimes the other.

The ideas involved in the two cases are of course fundamentally different. DARWIN'S view, although he never definitely formulated it, was that it was these occasional single variations which brought about the continual differentiation of living forms. In short, the essential process in the production of new forms is the gradual accumulation by natural selection of these small changes, provided they are useful.[1]

WALLACE'S view is that the material for species-forming selection is furnished by fluctuating variability; and that these infinitesimal differences are gradually heaped up in the same direction until ultimately they attain the dimensions of specific differences.

Even when proof can be brought forward, as it can in the case of many cultivated species, that plants are different from what they were one or two thousand years ago, it can scarcely ever be determined historically whether they favor the former or the latter of these two views. Those cases in which the sudden origin of a new form was observed and described by contemporaries, are the exceptions: and they tell in favor of DARWIN'S view, and never in favor of WALLACE'S.

And if it is impossible to discriminate between the two historically, how much less is there any hope of a verdict by the method of analogy, when there are no definite facts to go upon.

This being the case, we pass on to the consideration

[1] *Life and Letters,* II, p. 125.

of the second part of our question: what may be expected in the future as the result of continued selection.

It is generally assumed that individual variability is unlimited, moreover that as a result of continued selection in any direction variation continues to extend in the same direction. But this assumption is based on no empirical foundation whatsoever. The experiments of breeders, particularly those on acclimatization tell in favor of strictly limited (although agriculturally highly important) changes only.[1] The one thing about which there is absolutely no doubt whatsoever in this question, is the fact of regression: the definite backsliding of the mean of the race as compared with the extreme individuals chosen as seed-bearers.

By improved methods the selection process can be considerably accelerated, and the goal reached some years earlier. In practice important results have been obtained in this way, but they are not of such a kind as to be any help in this discussion.

I have already had occasion to remark once or twice that our knowledge of regression is very scanty, considering the great importance of the phenomenon: and that much remains to be found out about it. If it should turn out that as a result of continued selection the yearly reversion became gradually smaller we should have a result of extraordinary importance for the theory of selection. If the contrary happened, this theory would have to be definitely abandoned. And so long as a decision is wanting, the theory evidently lacks the necessary foundation.

The data that I have been able to collect tell in favor of the view that the maximum change which can be

[1] Cf. the following sections.

effected, is attained as a rule after 2 or 3 generations or sometimes after 4 or 5 or perhaps a few more. We are of course speaking of the improvement of a single character. In practice where one is concerned with several or more characters the process of selection may of course last much longer. And this is true even when improved methods render possible a more rigid selection from vast numbers of individuals, as in the case of beet culture where however one is usually dealing with fractional percentages.

In scientific experiments, with a single character in view, the duration of the period of selection is in my opinion to be placed as a rule at from 2 to 4 generations.[1] There is no point in continuing the experiment further unless one wishes to arrive at some decision on the question of regression which we have just been discussing.[2]

I am convinced that great harm has been done by this exaggeration of the length of the process, since it must have deterred many investigators from instituting experiments of this kind.

I shall now briefly recapitulate some such experiments gathered from the early literature on this subject. The first I refer to is the well-known essay of P. P. A. Lévêque de Vilmorin on the culture of the wild carrot (*Daucus Carota*).[3] He succeeded in less than 5 generations in improving the wild form until the roots were

[1] Cf. Fritz Müller's breeding experiment with maize: *Kosmos, loc. cit.*

[2] A well-known practical difficulty is presented by the fact that it is only after cultivating a plant, which is new to one, for a considerable number of generations, that one gets to know its needs in the matter of cultivation, manure, artificial fertilization, selection, etc.

[3] L. De Vilmorin, *Notices sur l'amélioration des plantes par le semis*, 1886; cf. pp. 10-12. Also Carrière, *Gardeners Chronicle*, 1865, p. 1154.

fleshy and they were as good vegetables as the ordinary cultivated carrot. In the same way CARRIÈRE developed in five years from the wild radish possessing small inedible roots a vegetable weighing from 3 to 6 hundred grams.[1] Again BUCKMANN found that the roots of the wild parsnip could be quickly increased in size by selection.[2]

We may conclude therefore that it does not take more than a few years to reach that point which remains constant in cultivation if selection is not slackened.[3]

At the beginning of this section we noted as the second principle of selection, the belief that the result of selection can persist independently of selection.

Now, it is manifest that specific characters are absolutely independent of selection. I am referring of course to the mean characters of elementary species, for the deviations from the mean are themselves the material for selection. Over 200 species of Draba verna are known; these come true to seed and persist as such independently of selection even when they are cultivated side by side in the same garden. This is also true of very many "species." BATESON has rendered good service in his great book *Materials for the Study of Variation* by having directed the searchlight of criticism on these weak points in the theory of selection. He challenges this theory to explain how the undeniable discontinuity in the series of species can have arisen from the continuity of ordinary variation. No such explanation has been offered. For artificial selection does not lead to the origin

[1] J. COSTANTIN, *in Bull. Scientif.* de GIARD, 1897, p. 499. Compare also LINDLEY, *Theory of Horticulture*, p. 313.

[2] DARWIN, *Das Variiren der Pflanzen und Thiere*, I, p. 408.

[3] If the selection stops the plants revert to the wild form, and this also in a short time.

of independent types. "Every race of plants possesses only a low degree of constancy," says one of our most considerable agricultural authorities, Prof. KURT VON RÜMKER.[1] Without a continuation of selection they would soon lose their good qualities. In this respect they behave quite differently from a true species or constant variety.

There is no need for me to go further into this matter now, for I shall make it my business in the following paragraphs to point out what the experience of breeders can teach us on this point.

Finally I should like to discuss a very instructive example more thoroughly. I refer to the important observations of R. VON WETTSTEIN on seasonal dimorphism as a point of departure for the origin of species in the vegetable kingdom.[2] He deals with the genera Gentiana, Euphrasia, Alectorolophus (Rhinanthus). In the alpine meadows there occur in the case of many species of these genera two forms (varieties, subspecies, or elementary species) of which one flowers early and the other late. Moreover the early and late flowering forms of one pair are usually distinguished from one another by a series of further characters of the value of the differences between elementary species.

The time for mowing the grass in Central Europe falls between the flowering season of these two varieties. The early kinds ripen their seeds before this time; the later only begin their main growth after it.

The work of VON WETTSTEIN clearly shows that these species are associated in pairs and has proved that

[1] *Der wirthschaftliche Mehrwerth guter Culturvarietäten,* 1898, p. 136 of the offprint.

[2] *Berichte d. d. bot. Gesellsch.,* 1895, Bd. XIII, p. 303, and *Bot. Centralblatt,* 1900, No. 1, p. 15.

their separation was brought about by selection in the field. But that obviously does not settle the question as to whether these pairs have arisen by a process of gradual change or of sudden convulsion. These most important results considered in relation to the subject under discussion not only do not enable us to decide, for this particular case, between the mutation and the selection theory, but they also leave undecided the question whether (supposing the latter is true) the change was completed in a few generations, or was attained in the course of centuries.

§ 10. ACCLIMATIZATION.

Acclimatization is perhaps the best touchstone that can be used for testing the efficacy of the doctrine of selection. Selective breeding, which so often has to overcome natural selection, in this case works in accord with it. Moreover there is a strong agreement between artificial and natural acclimatization, whether this latter be the result of migrations of organisms or of essential changes in their climatic or œcological environment.

It is here therefore that we have most chance of finding out how much natural selection is capable of doing.

But the harvest turns out very scanty—so scanty indeed that the upholders of the doctrine of selection are loath to assign it a very prominent position among their arguments.

In practice the process of acclimatization is extraordinarily complex. In most cases we are only concerned with finding out whether such and such a species can grow in a new locality or not. And we find that either the difference between the old and the new locality has

no effect or that partial adaptations appear, of the kind with which we are acquainted through BONNIER'S experiments with alpine plants.[1] It may also happen that the species in its old locality consists of a group of subspecies of which some are suited to the new climate while some are not; in such a case all that remains to be done is to find out which are suited and which not.

On the theoretical side we may apply the theory of acclimatization to the solution of the problem of the distribution of a single species over vast regions, as for example in the case of maize in America. The climate of a locality determines the subspecies which inhabit it, sometimes favoring a tall luxuriant plant laden with large ears heavy with seed, sometimes small plants ripening in a few weeks with little ears and seeds (Fig. 20).

But whether such subspecies have arisen by gradual selection or by mutations can of course no longer be determined empirically.

The process, however, which is really interesting to us here, is the conscious or unconscious selection of individuals which are best adapted to the new conditions: in other words the establishment of a new race by means of the material supplied by fluctuating variation.

Before passing on to consider this case in detail I should like to mention an example which more than any other shows how careful we must be in using practical experience for the solution of scientific problems. It is the case of a result obtained by one of the most distinguished growers in Germany, J. METZGER, and of its scientific application by DARWIN himself, It is the case—so well known and so often quoted—of the transformation of an American variety of maize into the ordinary

[1] Compare also § 17, pp. 144-146.

maize of Baden, within three years after its introduction into Germany.

DARWIN quotes METZGER's *Getreidearten,* translating word for word. METZGER's *Landwirthschaftliche Pflan-*

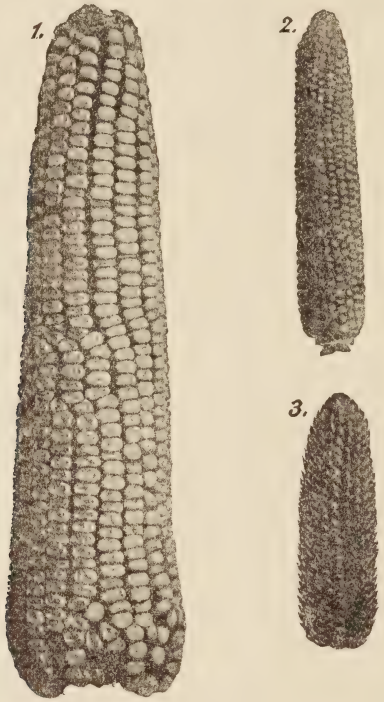


Fig. 20. Ears of Maize of Commerce. All the figures reduced on the same scale (1/3). 1. Giant yellow Dent field corn. 2. Miniature maize (Zea gracillima). 3. Pop-corn (white Rice Maize).

zenkunde lies before me; it contains the description of the observation on page 208 in the first volume.[1] DARWIN calls this case *the most remarkable instance known*

[1] DARWIN, *Variations of Animals and Plants Under Domestication,* I, p. 340. METZGER, *Getreidearten,* p. 208, *Landwirthschaftliche Pflanzenkunde* (? the same work) 1841, I, p. 208. Cf. also WALLACE, *Darwinism,* 2d. ed., p. 419.

to me of the direct and prompt action of climate on a plant, and WALLACE regards this transformation as a result of *that "reversion to mediocrity" which invariably occurs and is more especially marked in the case of varieties which have been rapidly produced by artificial selection. It may be considered as a partial reversion to the wild or unimproved stock.*

Let us now see what METZGER says. He is dealing with a white broad-seeded American Maize, the *Tarascora Corn* from St. Louis.

"We cultivated this form[1] and got stems 12 feet high in the first years and only a few ripe seeds of which the lowest on the cob were like the original form whilst the upper ones appeared to lack the depressions and to show features like those of the European Maize.

"We sowed the seeds from these next year and obtained plants from 9 to 10 feet high whose seeds ripened earlier. The seeds were noticeably larger than in the previous year, the depression on the surface had already disappeared and the beautiful white color appeared darker and dirtier. Some seeds were yellow; and their round form was just like that of our own maize and betrayed no signs whatever of the characters of the form from which they had sprung. In the third year of the cultivation all the characters of the American form had disappeared and the American maize had been transformed into subspecies 5 form B.[2] We obtained another lot of the seed of this same variety which in the third year approached the same subspecies 5, B and exactly resembled it after six years of cultivation. This maize is now

[1] From the description the variety must have belonged to the Dent corns.

[2] Large White European Maize. *Zea praecox L.*, p. 213.

often grown in our neighborhood and can be distinguished from our common form only by its somewhat more "branching habit."

I can find nothing—not even a suggestion—in METZGER'S account about the cause of this transformation. But any one having an acquaintance with hybridization and the so-called running out of cereals will see that METZGER'S case is not an instance of the transformation of a race by climatic influences. The cultures of the Tarascora maize stood between other kinds and were obviously liable to be fertilized by the pollen of these through the agency of the wind. Some of the seeds would in that case give hybrids which could give rise in the third generation to pure European maize.[1]

The hybrids and their pure European progeny would be likely to supplant the foreign strain which would be less adapted to the climate of Baden; and this would take place in a much shorter time than one would be inclined to think. And inasmuch as this supplanting of one sort by another has been so often mistaken for the supposed transformation of a species or even for the creation of a new one it is worth while to cite in some detail a few examples which may be selected from RIMPAU'S celebrated work: *Risler's Weizenbau.* The first example is an observation of RISLER;[2] the second is due to RIMPAU himself.

RISLER describes a case of degeneration of *Galland* wheat during the first few years after its introduction into his estate at Calèves on Lake Geneva in Switzerland. The ears of this variety, when they make their

[1] A more exact discussion of this point will be given elsewhere.

[2] EUG. RISLER, *Der Weizenbau.* Translated by W. RIMPAU; Thaer-Bibliothek, P. Parey, 1888, pp. 73-74.

first appearance, have beards; but lose them when they ripen. In the first year in the new environment practically all the ears with very few exceptions had this character; but in the second year already half were beardless, whilst in the third year the latter formed the great

Fig. 21. Rough Awned Wheat of Rivett and ordinary German Field Wheat.

majority; they also differed from the original form in the fact that their seeds had a horny instead of a mealy texture.

To determine the cause of this degeneration Risler

sowed alternating rows of Galland wheat and beardless wheat; and it was discovered that the former suffered more from the cold of winter than the latter and that it ripened from 8-14 days later; these two differentiating characters sufficed to enable the small initial admixtures of the beardless wheat to get the upper hand within three years.

RIMPAU'S observation concerns the rough wheat (RIVETT'S *Bearded,* Fig. 21) of which it is often asserted that it easily degenerates and that after a few years it always contains a larger or smaller proportion of beardless examples. But when kept absolutely free from admixture, as in RIMPAU'S experiments in Saxony, this form remains perfectly true; as indeed it has done in Scotland for over a hundred years. "But it was more liable than any of the varieties of wheat we grow to suffer from the winter, and as it develops later in the spring than all other sorts it is easy to understand that all chance admixtures, which are unavoidable in cultivation on a large scale—and are apt to be introduced by the use of farmyard manure—will multiply much more rapidly and soon obtain the upper hand."[1]

The results of experiments in acclimatization, therefore, can only be used as scientific evidence when the danger of crosses, or of degeneration by the chance admixture of native races is absolutely excluded.

The best examples have been collected by SCHÜBELER who is himself responsible for some of the results in his collection.[2] They relate chiefly to the acclimatization of

[1] It is well known that in bad years *Avena fatua* multiplies rapidly among oats; it contributes nothing to the yield. GODRON, *De l'Espèce,* I, p. 163.

[2] SCHÜBELER, *Die Pflanzenwelt Norwegens,* 1875. Also, *Die Culturpflanzen Norwegens.*

maize and other cereals to northern localities and to mountain districts, in other words to the extension of the culture of cereals into higher altitudes and latitudes. This end is usually attained by shortening the period of growth and by being content with a correspondingly smaller harvest. In the case of chicken-maize, for example, the duration of life was shortened from four to three months in the course of five years. The same happened in the case of rye and wheat. During the first few years of the culture it is only the individuals that flower first that ripen their seeds, and this of itself brings about an effective process of selection. In the same way, though in this case deliberately, the flowering time of *Chrysanthemum indicum* has been partly shifted back to July and partly advanced into the following February. The same is true of innumerable garden plants, of various varieties of cucumbers, and so on.

But the available experience on acclimatization does not go much further than this;[1] and we may be quite sure that new specific characters have never arisen in this way.

§ 11. SUGAR BEETS.

Sugar beets afford the finest example of the process of artificial selection. In no other plant under cultivation has the technique of selection reached so high a pitch of perfection; in no other is the method so sure or the result so certain. There is now no sale for beet seed which has not been the result of careful selection.

Experiments in the selection of sugar capacity began about 1850. This instance shows best, therefore, what

[1] A review of the subject is given in J. Costantin's splendid work: *Accomodation des plantes aux climats froid et chaud.* Bull. Scientif. de Giard, XXXI, 1897, p. 489.

can be achieved within half a century by continued selection in one and the same direction, hand in hand with continual improvement of method.

Progress has been enormous: the average content of the common beet, which at first was a matter of 7-8%, is now double that amount. Shape, size, and weight, the character of the leaves and especially the reduction in woody tissues have all been the object of selection, and have made the beet much more valuable from the industrial point of view.

All this has been done by selection of the best individuals afforded by ordinary fluctuating variation. Neither spontaneous variations nor crossings have played any part in it. We are dealing here with the process in its simplest form.

This is not the place to praise the genius of Louis Vilmorin, the founder of the method, or the achievements of his numerous successors especially in Germany. Nor need I describe the marvelous technical process by which it is possible to determine the polarization indices of more than 100,000 beets in a few weeks.[1]

On the contrary I am only concerned with showing how little value these splendid results have in the discussion of the process of the origin of species. On the botanical side no better argument for the theory of selection could be adduced. Yet in this case there is nothing which is in the remotest degree like the origin of a new species nor even anything that could lead us to expect that any form of the systematic value of a species could arise in this way.

[1] I particularaly recommend to the scientific reader the study of Prof. Kurt von Rümker's short and clear paper: *Die Zuckerrübenzüchtung der Gegenwart.* (Blätter für Zuckerrübenbau, 1894, pp. 1-48.)

Of course I am not speaking of the origin of the sugarbeet itself. We know as little of its origin as we do of the origin of the other varieties of beets. The Romans probably had only two sorts which they used as vegetables, which they cultivated in their gardens and collected in the wild state.[1] At the beginning of the nineteenth century there were numerous kinds. The question arises: did they originate from the older forms in culture, or were they first found as distinct subspecies in nature? We do not know. That they had a common origin we do not doubt, but whether they originated before or during cultivation remains a mystery.

The beet with which VILMORIN began his work half a century ago must be regarded simply as a starting point; artificial selection is responsible only for what it has given rise to.

As far back as 1830-1840 VILMORIN had selected his beets according to their external form. In 1851 he determined the saccharine contents of single roots and found that it varied from 7-14%, but the troublesome nature of the methods of estimation available at that time only permitted of the determination of comparatively few instances. He discovered the best beets by their high specific gravity in salt solutions, sowed the seeds which they produced and got beets with 21% sugar in the second generation.[2]

These figures (7-14-21%) are very important in this connection. It must be remembered of course that they cannot be compared very exactly with the results of recent work because the method has become much more

[1] PLINIUS, *N. H. Lib.* 19. See also COLUMELLA and CICERO (Note of 1908).

[2] L. LÉVÊQUE DE VILMORIN, *Notices sur l'amélioration des plantes par le semis.* 2d edition, 1886; see especially p. 27.

simple and precise, especially since the introduction of the use of the polariscope.

But it is more likely that VILMORIN's figures were too low than that they were too high.

1874 was the first year in which the method of polarization was employed and the selection based on the results of this method. The normal contents ranged at that time between 10-14%. In bad years with a mean of 10%; in good ones it was from 12 to 14%.[1] Even cases of 9.5 and 17.5% were not rare.[2] From 1878 to 1881 the method of polarization spread in Germany and Austria; I need only mention the names of DIPPE of Quedlinburg, RIMPAU, HEINE and the Klein-Wanzleben factory. The progress was slow but sure. In most factories the beets are examined only comparatively, except in the case of the best ones, in which the polarization index was actually determined. In the works of Messrs. KUHN & Co., however, at Naarden (Holland) this index has been directly determined every year for over 300,000 plants. Through the kindness of these gentlemen I obtained in 1896 the indices of 40,000 roots; they made a very beautiful curve with a mean at 15.5% (Fig. 22.)

Selection is then carried out with reference to these figures in such a way that sufficient plants are always available for seed. The result of polarization determines the limits of the groups. I shall now give some figures for 1892. Roots with less than 14% were not planted for seed. Those with from 14-16% formed the seed plants for commercial seed; there were 20 to 30 of

[1] LANGETHAL, *Landwirthschaftliche Pflanzenkunde*, III, 1874, p. 69.

[2] *Jahresbericht der Zuckerindustrie*, Vol. 9, p. 39 etc.

these in every 100 plants examined. Those with from 16-18% became the seed plants for the special race, the so-called élite race from whose seeds the beets were produced which would be tested in the next generation. In 1892 there were among 180,000 polarizations only four instances of a higher percentage than 18% in the

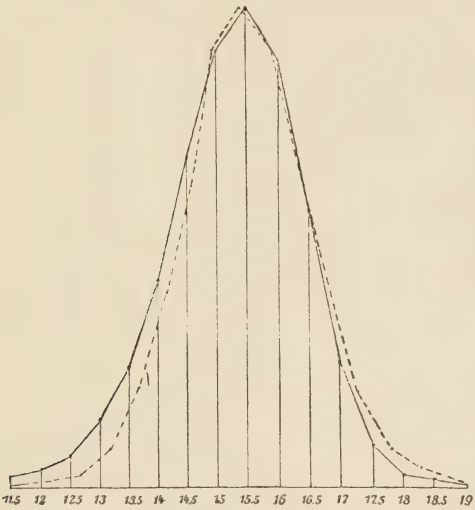


Fig. 22. Variation in the Amount of Sugar in 40,000 Beets.[1]

above mentioned factory. Since that time the annual number of polarizations as already mentioned has reached about 300,000; and the maximum percentage has

[1] The polarizations in question were carried out from January 23 to February 5 in 1896 and gave the following figures:

Sugar % . . .	12	12.5	13	13.5	14	14.5	15	15.5
Individuals . . .	340	635	1192	2205	3597	5561	7178	7829
Sugar % . . .	16	16.5	17	17.5	18	18.5	19	
Individuals . . .	6925	4458	2233	692	133	14	5	

Individuals with less than 12% have been excluded from this series. The dotted line is the theoretical curve according to QUETELET'S law, $(a+b)^{20}$; the discrepancy between it and the actual curve on the left side is probably due to the presence of some faulty beets.

mounted to 21%, and the other figures have risen correspondingly. Commercial beet grown from this selected seed, has on the average 13 to 14% sugar.

Without underrating the high agricultural significance of these results we must nevertheless face the fact that there is very little in them which can serve as a basis for a decision of the question of the origin of specific characters. We cannot be certain whether after selection for fifty years, i. e., for 25 generations, the upper limit of the range of variability has been essentially extended or not. It so happens that this limit—21%—is the same in VILMORIN's instance (1853) and in the works at Naarden (1892-1898), but there are other races under different conditions of cultivation, whose limit is stated to be as high as 26%. The wider range of modern polarization work with beets evidently gives a chance of higher percentages.

The average product of a field has certainly increased from 7-8% to 14-16% and more. But this improvement is dependent on the continuation of selection; and it is only by this means that it has reached this pitch. Every sugar manufacturer knows that selection is an indispensable condition of a satisfactory harvest. It is true that, for the purpose of obtaining the necessary quantity of seed, a so-called intermediate generation is interpolated between polarization and seed-harvest: but if more than one or at most two (and this happens very seldom) of these are introduced the advantage gained by polarization and selection is lost. By no manner of means is the improvement independent of selection; on the contrary the promise of more sugar can only be fulfilled by a further perfection of the method of polarization and by continued efforts on the part of breeders.

Since the method of polarization was introduced the progress of the sugar beet has been slow but continuous. But it must not be concluded from this that the present maximum could not have been reached in a few generations. At any rate we are not justified in deriving this conclusion from the evidence at hand. Progress has obviously been due to the steady improvement in methods of selection. This has consisted first in the invention of the boring cylinder which enables us to polarize directly the beets to be selected; VILMORIN and his immediate followers had to sacrifice the whole beet to their chemical analysis, and then to select others, resembling the best ones in specific gravity, for cultivation. And secondly by employing larger and larger groups to choose from, (in the best factories every year more than 100,000 beets). For it is evident that the larger number there is to choose from, the greater chance is there of finding desirable ones.

Beets have been selected not merely with regard to their saccharine contents but also with regard to their external features. This takes place in the field at the time of harvest, that is to say, before polarization. In most factories about $\frac{9}{10}$ are thrown away in this process and only $\frac{1}{10}$ saved. Breeders are of the opinion that on the whole this $\frac{9}{10}$ includes plants inferior in respect to their saccharine contents and that by this selection a beneficial effect on the percentage of sugar itself is brought about.[1] In this preliminary selection attention is paid first to the leaves; the features dealt with being their shape, their size and the angle which they make with the zenith, as well as the general features which control assimilation, transpiration and the non-retention

[1] v. RÜMKER, *Zuckerrübenzüchtung*, p. 5.

of rain water. The various kinds of beet, in which selection has had different objects in view, can be recognized by their foliage in the field. The form of the root is very important; it should be unbranched; the more like the roots are to one another the more easily can they be dealt with. The dimensions of the stem, or the head as it is called, and many other points have all to be considered and especially the size or the weight, of the whole beet.

Individual breeders pay attention to trivial characters as for example the red color in the seedling with the object of facilitating the detection of impurities in their strains in the field.

It is absolutely essential to keep one's eye on all these points in every generation. In the case of no single character can selection be relaxed. Any disregard of these rules on the part of the breeder would soon lead to a degeneration of the whole race.

"Each race of plant possesses only a very small degree of constancy." Herein lies the difference between the improved race and the species. This already quoted expression of Von Rümker[1] sums up clearly and concisely the whole significance of agricultural results in their bearing on Natural Selection.

§ 12. CEREALS.

Next to the sugar beet the cereals have furnished the most important material in connection with scientific and practical experiments in selection, though in the latter case the general conditions are much less simple.

Modern efforts to improve the races had to start

[1] Von Rümker, *Der Landwirthschaftliche Mehrwerth, loc. cit.*, p. 136.

with a vast assemblage of varieties of unknown origin. According to NILSSON, every larger or smaller "species" includes hundreds of such varieties. In the second place one of the tasks of rational breeding is to cross these sorts with one another as much as possible in order to combine their characters in the particular way which seems most desirable for each separate case. The origin of these hybrids is in most cases unknown, or at best the information concerning them is either incomplete or uncertain. The excellence and variety of our cereals can only be attributed in a small degree to the direct effects of selection.

In his excellent treatise *Anleitung zur Getreidezüchtung* VON RÜMKER distinguishes between empirical and methodical selection.[1] Empirical selection is the general process which every intelligent farmer ought to practise; it is carried on on a large scale in certain districts, as for example the Probstei, where the entire harvest is sold as seed. Empirical selection consists at least in choosing the best piece of the field, and in growing the seed for the next year on it. Or the harvest is threshed, the largest and heaviest grains are separated from the less valuable ones by a hand sieve or by a centrifugal machine, and kept for sowing. Thirdly a sorting by ears is carried out at mowing time and consists in setting aside the beast ears borne by the strongest halms in sufficient quantity to provide for the élite race for the ensuing year.

The object of empirical selection is to keep the different kinds pure and to put a stop as much as possible

[1] DR. KURT VON RÜMKER, *Anleitung zur Getreidezüchtung auf wissenschaftlicher und praktischer Grundlage*, Berlin, 1889. Compare also RISLER-RIMPAU, *Der Weizenbau* in the Thaer-Bibliothek, 1888.

to the degeneration resulting from the admixture of inferior varieties (cf. pp. 96-98). Even if only for this reason it ought never to be slackened. Then again it is concerned with keeping the kinds which have been improved by selection up to the mark; without it they would steadily deteriorate and necessitate the purchase of fresh seed too often. Lastly it adapts varieties to local conditions of culture: no two localities are alike with regard to soil, climate and manure.

In certain districts (Probstei, Ostsee, Hanna and the Tirol) empirical selection has been practised for more than a century on a large scale by the majority of the peasants engaged in growing cereals. As a result they sell their whole crop as stock seed at a high price. But in order to keep up the good reputation of their varieties it is necessary that selection should continue without ceasing. It is very difficult to tell whether this form of selection leads to a further amelioration of these races because real improvements undoubtedly are made from time to time as the result of improved methods of selection. But the essential fact is that no race which is independent of selection has yet arisen in this way.

Methodical selection is based on an entirely different principle. It is carried on by a few men at the head of their profession and its object is to put new and valuable races on the market. Each such race consists of two parts. First the pedigree or the so-called élite and secondly seed for the market and for the trade.

The originator of a race of this kind keeps the pedigree stock on his own property. This stock does not amount to more than a few or at any rate to more than a few hundred individuals in a year, and is the product of the selected seeds of the previous generation. Of the

seeds which it produces only the very best are kept for sowing for the continuation of the stock. The commercial race is not in the strict sense of the term a race, for the successive generations which compose it are not genetically connected. Each generation begins as a lateral branch of the main stem; the first harvest, after the seeds for the pedigree stock have been set apart (and after inferior seeds have been rejected) is grown on special fields for at most 2 or 3 generations to produce the quantity of seed required for the market. In every successive year, therefore, the stock for the market starts as a new branch of the main stem; it is not for two or three years after improvements appear in the latter that they are obtainable in the former.

It obviously follows from this that the race never becomes independent of selection, as a true species or subspecies does. There are, of course, beautiful examples of subspecies among cereals, but they have not arisen by selection. Patrick Shirreff's older varieties are examples of these; they are independent of selection and often so good that they cannot be improved by it—e. g., the *Talavera* wheat. A sharp distinction must therefore always be made between species and subspecies on the one hand, and races on the other.

The greater the improvement of a race has been, the more does it deteriorate in ordinary cultivation; its seed can only quite exceptionally be used for further crops.[1]

Methodical selection is of two essentially different kinds. Their most distinguished exponents were Hallett of Brighton (England) and Rimpau of Schlanstedt (Saxony). I shall now endeavor to give an account of

[1] I shall deal with this question in more detail in § 14 of this part.

their methods, so far as the space at my disposal allows.

HALLETT[1] grew his pedigree stock under the most favorable circumstances possible because he was convinced that manuring, open position and generally favorable conditions of life call forth the variations desired. To start a culture of this kind he sought, in the best field of the kind of wheat in question, for the best ear he could find and sowed its seeds in good garden soil as early as possible, allowing plenty of space between the plants. These produced strong richly branched plants with about 100 stems and about 3000 grains per plant and on the average about 100 grains per ear. This extraordinary advance is necessary for the improvement of the race, but it is obviously lost if the new race is grown in the field under normal circumstances. In the pedigree stock however it persists. From this the best ears on the best plants were yearly chosen with the greatest care; and of these only one ear was used to supply seed for the continuation of the experiment. As a result of this, regular improvements took place in the yield and HALLETT believed that these did not diminish when the plants were cultivated in the field.

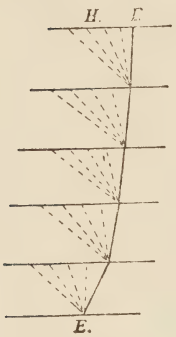


Fig. 23. Scheme to show the relation between the selected stock and the so-called commercial stock. The continuous line (*E-E*) indicates the line of descent of the former, in successive years; the dotted lateral branches furnish either directly or in the course of a year or two the commercial stock, *H*.

There is no question that improvement takes place

[1] FREDERIC F. HALLETT, *On Pedigree-Wheat as a Means of Increasing Crop*. Journal of the Royal Agricul. Soc., Febr. 1862.

in the experimental garden; the question is whether this is maintained in the field. To decide this we must look to the lateral branches of the pedigree which are given off every year, in which the seed is increased in quantity for the market as explained above. It is not every culture that succeeds (e. g., the *Original Red Wheat*); but it is only about the successes that records are published.

The value of HALLETT's work is proved by the commercial success of his races.[1] But he seldom gives data of any value for scientific purposes. Several of his productions have found a wide sale, especially in England, as for example HALLETT's *Pedigree wheat, Victoria White* and *Golden drop,* three famous varieties of wheat. His *Chevalier barley* and his two kinds of oats *Pedigree White Canadian* and *Pedigree Black Tartarian* are also well known.

HALLETT asserts that, for each sort, the rate of improvement gradualy falls off year by year until at the end of many years the race reaches its maximum and becomes

Fig. 24. HALLETT's *Pedigree Wheat,* viewed from the narrow and from the broad side. Below are shown (*a*) grains from the ears of this wheat and (*b*) grains of ordinary wheat (compare Fig. 21, p. 97.)

[1] *Pedigree alone has increased my crops from* 25-30%. HALLETT, 1868.

constant. But of course it will not remain so, if it is not subjected to continuous selection.

Fig. 25. Schlanstedt Giant Rye, bred by W. RIMPAU. *b.* Grains of this strain; *c.* ordinary grains of rye on the same scale of reduction.

RIMPAU'S method is quite different. He grew his pedigree stock under circumstances which resemble the normal conditions of life in the fields as closely as possible. The plants were however grown somewhat further apart and were treated with greater care. At the beginning of the experiment he plucked a handfull of the best ears, sowed them on a small plot set apart for the purpose and picked the best ears from this at harvest time, for seed for the next élite generation.

RIMPAU and VON RÜMKER insist very strongly that plants grown under unusually favorable circumstances should not be chosen for selection; ears found at the edges of fields or on specially luxuriant patches should most certainly not be used for this purpose.[1] Their proper-

[1] VON RÜMKER, *Getreidezüchtung*, 1889, p. 58.

ties, however desirable, are not heritable. I have failed to ascertain whether this opinion, which is so strongly in opposition to HALLETT's has been arrived at as the result of experiment. But it is obvious that the progeny of the ears picked at the edge of the field or in luxuriant patches would require similar conditions of space and soil for their full development, and as they would not get them we should be raising a variety that was not adapted to its environment. For the improvement of races consists primarily in the adaptation of the plants to the conditions in which they live; the real point about modern strains of cereals is that they can get more out of the amount of manure which is usually applied, than the old strains. A race is of little value except under those particular conditions to which it is adapted; how far it will spread in general cultivation depends on how widely distributed these conditions are.

There is therefore a greater likelihood of raising a valuable race by RIMPAU's method, than by HALLETT's; but it takes a longer time to arrive at the result. And even RIMPAU did not succeed with every attempt; for example he states that he spent a great deal of vain labor in trying to improve the ordinary brown saxon wheat by his method.[1]

RIMPAU's Schlanstedt Rye is well known to every farmer.[2] He began working with it in 1867. When I visited RIMPAU on his estate at Schlanstedt in 1876 he showed me his pedigree culture which even then furnished the seed for the greater part of his domain. Since 1886 he has been in a position to sell his whole harvest as seed.[3] The race has general recognition and has con-

[1] RISLER's *Weizenbau*, p. 66 note.

[2] v. RÜMKER, *Getreidezüchtung*, p. 74. [3] *Weizenbau*, pp. 65-66.

sequently extended over Germany and the north of France,[1] and is now admitted to be one of the best European cereals.[2] Ears and grains are about twice the size of those of other sorts of rye; they ripen earlier and, what is far more important, give a much larger return per acre.[3]

In this case as in the previous ones, incessant selection and plenty of manure are the conditions which are necessary to keep the race at the level which it has reached. Avidity for manure is, according to Risler-Rimpau, a feature which distinguishes improved races from constant varieties.[4]

This improvement of races,[5] as now practised in agriculture, has, however, of late appeared in a wholly different light through the practical researches of Dr. Hjalmar Nilsson of the Swedish Agricultural Experiment Station at Svalöf.[6]

He discovered that cereals and other agricultural crops consist of far larger numbers of elementary species, than was hitherto supposed. Out of every so-called variety hundreds of such minor types can be isolated, which as a rule prove constant at once after such isolation. Exceptions are offered by casual hybrids, which may split up, after which the products may, however,

[1] Schribaux, *Seigle de Schlanstedt,* Almanach du Cultivateur, 1892, p. 66.

[2] See, e. g., the seed catalogue of Vilmorin-Andrieux in Paris.

[3] The rye of Rimpau has since been surpassed by that of *Petkus,* produced by Von Lochow (Note of 1908).

[4] *Weizenbau,* p. 80.

[5] The following paragraphs were added to the translation, 1908.

[6] Cf. *Sveriges Utsädes förenings Tidskrift,* Years 1892-1907, Vol. I-XVI, and *Die Svalöfer Methode zur Veredlung landwirthschaftlicher Kulturgewächse und ihre Bedeutung für die Selektionstheorie,* Archiv für Rassen- und Gesellschafts-Biologie, Jahrg. 3, pp. 325-358. 1906.

also give rise to constant races. Within each cultivated variety the number of differentiating characters may be small, but the large number of elementary forms may be due mainly to the vast number of ways in which they may be combined. Probably these subspecies have arisen in the fields by casual mutations and subsequent free crossing; such crosses being, as a matter of fact, very rare, but occurring often enough to give rise in the lapse of years to almost all possible combinations of characters.

The diversity among these elementary forms is so large, that it answers almost all the claims of practice. This fact is of the highest practical interest, since now it is only necessary to search for the desired types, to isolate them, to estimate their value and to multiply them to the amount required. No slow improvement, no repeated selection is necessary; the fluctuating variability within the elementary species being moreover so small, as hardly to afford material for such work.

This search for useful elementary types must be carried on in the fields at the time just before the harvest. The ripe ears are selected and their grains sown separately for each parent-plant. From these the new races are started. At the time mentioned many valuable characters can be judged, but others cannot, or cannot be estimated with a sufficient degree of accuracy. This difficulty, however, has been met by another discovery of Nilsson,[1] viz., the correlation between botanical and agricultural characters. On the ground of this, the first selection is made by the aid of botanical marks, which are discernible in the ripe ears, and the subsequent com-

[1] For more details see *Plant-Breeding, Comments on the Experiments of Nilsson and Burbank,* Chicago, 1907.

parative study of the isolated races is made by both botanical and economically valuable characters. Hundreds of different types can be isolated from the harvest of a field in this way if one is only thoroughly acquainted with the correlative value of these apparently unimportant characters. For instance the propensity towards layering may be estimated by the density of the ears; shortness of internodes being closely correlated with stiffness of halms. The value of barley for the purposes of the brewers is indicated by the kind of hair on the scales, crisp hairs denoting the best qualities of the grain. On the basis of this correlation a new brewers' barley has been isolated at Svalöf, not from the ordinary Chevalier-barley, which is much subject to layering in Sweden, but from the Imperial barley, which is not a brewers' barley at all but has very stiff halms. This new type answers the demand of practice especially in Middle Sweden, where it is now almost exclusively cultivated for this purpose. It is called Svalöf Primus Barley.

Correlation, as understood at Svalöf, does not mean that two characters are inseparable, but only that they are found to accompany each other in the majority of the cases, i. e., in 90 out of 100 instances. Mother-plants selected in this way, have therefore to be subjected to a subsequent selection by means of their progeny.

The new races, which have been isolated and put on the market from Svalöf in this way include 7 types of winter wheat, 1 of summerwheat, 8 of barley, 5 of white oats, 2 of black oats, 4 peas and 3 vetches. The first of them was brought out in the year 1897. Numerous new types have since been isolated but are as yet, still in preparation.

By means of these facts the common agricultural

method of repeated selection and slow improvement may be explained in a way which shows its complete agreement with the theory of mutation.[1]

Such a selection was begun by choosing a handful of ears from the best specimens of the variety which it was intended to improve. From these a race was started, in which the selection was repeated every year on the same principles. But according to the discoveries of NILSSON the first handful of ears must have been far from uniform; in fact it must have contained almost as many different types as there were ears. For even after a selection by the elaborated methods now in use at Svalöf, two apparently similar ears may give rise to wholly different races. In former years the similarity of the best ears chosen from a field, was therefore erroneously expected to give a uniform result.

From this point of view the real meaning of the subsequent repeated selection at once becomes clear. Every year, from among the motley group, those ears were chosen which most closely approached the ideal. In this way, slowly but surely, the mixture must become purified, till at last, after perhaps 10 or 20 years, it was reduced to only one of the constituent types of the first choice. As soon as this stage was reached, the race was pure and constant and independent of further selection, which now only played the rôle of permanently keeping it in a pure condition.

The slow improvement of agricultural races, which played such a large part in the selection theory of DAR-

[1] *Elementary Species in Agriculture,* Proceed. Americ. Philos. Soc., Vol. XLVI, 1908, p. 149. Cf. also: *Aeltere und neuere Selektionsmethode,* Biol. Centralbl. XXVI, No. 13-15, 1906; *La théorie darwinienne et la sélection en agriculture,* Revue scientifique, 5e Serie, Tome V, p. 445, 1906, and *New Principles in Agricultural Plant-Breeding,* The Monist, Chicago, 1907, p. 209.

WIN is thereby shown to be only apparent. In reality it is only an isolation of previously constant types. From horticultural practice it only differs by the fact that the races to be isolated are old constituents of long cultivated mixtures whereas in horticulture mutations are usually isolated as soon as they appear.

§ 13. THE LIMITS TO THE AMOUNT OF CHANGE THAT CAN BE EFFECTED BY SELECTION.

Selection does not lead to the origin of specific characters.[1] If I have succeeded in showing that this generalization is in accord with the facts of plant-breeding, the chief support of the doctrine of selection has been undermined. I propose therefore to summarize the most important parts of my argument in a series of short paragraphs.

1. *Linear Variation.* Statistical methods of dealing with variability are so generally employed at the present time that an acquaintance with their principles may be taken for granted. The chief thing however that we learn from these curves is that the characters vary only in two directions: *plus* and *minus*. The old-fashioned vague talk about variation of single characters in all directions has died a natural death. All variations in mass, and weight, and number (meristic variations) conform to this law.

The character can be diminished or increased, *but nothing new can arise in this way.* The differentiation of organisms in the main lines of descent consists in the development of new characters; and the materials for

[1] In men abnormal characters fluctuate; but they soon disappear and no new monstrous variety arises. See KOLLMANN in *Correspondenzblatt d. deutsch .Ges. f. Anthropologie*, 1900, No. 1, p. 3.

this are not supplied by the linear variation of characters which are already present.

2. *The Duration of Progress.* The view that linear variation is unlimited in the sense that the changes which can be brought about by selection in the course of centuries are greater than those which can be attained in the course of a few years, is absolutely without foundation. We are speaking of course of the improvement of a single character considered by itself. As a matter of fact, 2 or 3 years under favorable conditions, or 3 to 5 under ordinary ones, are quite sufficient. The further prosecution of selection serves merely to keep the race at the level which it had reached, unless special circumstances arise (see sections 6 and 7).

3. *The Limits of Selection.* There is just as definite a limit to selection as there is to linear variation. The limits of the latter can be extended by dealing with a greater number of individuals; but it takes an enormous increase in this number to sensibly extend these limits. It is the same with selection; but this at least has the advantage that the number of individuals dealt with can be diminished by discarding those of no value.

It is often stated that variation in a given direction can be increased by selection in that direction. Observations, or exact information in support of this statement are not given. There is of course an appearance of change owing to the elimination of the less valuable individuals. As a matter of fact in accurately recorded cases the very reverse is found to be the case; that is to say, that it becomes gradually more difficult to effect any change until finally it becomes impossible.

Darwin's view that plants increase in variability in the first years after they are brought into cultivation

probably owes its origin partly to the fact that the number of individuals is vastly increased during that period and partly to the frequent discovery of subspecies which previously had been overlooked.

4. *Regression.* Selection is succeeded by regression, which is great in proportion to the stringency of the selection which preceded it. However long the selection is maintained it is always followed by regression. It appears that much more than half of what was gained is lost after cessation of selection. The mean of the character so far as we know cannot be altered; regression always aims at the bull's eye of the specific character. I shall return to this point in the next section.

We may lay it down as a general rule that a doubling or a halving of the original mean is about the most that can be attained by selection. And usually one has to put up with much more meagre improvement.[2] The most conspicuous case of variability is the increase in fleshiness in fruits and roots, but this exception is only apparent.[3]

5. *The Instability of Races.* The chief difference between improved races and species, even the smallest elementary species, is the instability of the former and the stability of the latter. Races that have arisen by selection can only be preserved by continuing that process; it costs as much trouble to retain them as it did to obtain them. If selection of the race ceases, the characters of the race fade away. And the time it takes them to disappear is the same as it took them to appear. In a few generations they come; in a few also do they go.

[2] Compare the figures given in WALLACE's *Darwinism,* p. 81.

[3] The crab apple is more than half the size of most of our eating apples.

6. *Continual Improvement of the Method of Selection.* Commercial considerations demand a continual progress, partly in the actual improvement of stock, partly for the purposes of advertisement in order not to be eclipsed by competitors. This progress is effected in many ways, among which the most important from our point of view are the improvement of the method of selection and the practice of breeding with as many characters as possible in view at once. Every improvement in method renders a more effective selection feasible. But if after this the selection remains constant no further advance is possible.

7. *Improvement in Many Directions.* A scientific investigation should, if possible, be restricted to a single character. But the laws of correlation seldom allow us to follow this rule. Besides, the conditions of our investigations exert an unconscious selection in the garden, analogous to the so-called natural selection in the fields, inasmuch as the stronger manage to flower while the weaker do not. The practical breeder on the other hand pays attention to as many features as possible. And that is the chief reason why his experiments last so much longer. For it is not difficult to see that with a limited number of individuals it takes twice as many generations to deal with two characters as it does to deal with one. The greater the number of characters we handle, the slower shall we be in attaining our result.

8. *Adaptation to Special Conditions of Cultivation.* Every improved race is adapted to a special environment, of soil, climate and manure. That is why they are so local in their distribution and so fastidious. Many English races cannot stand the German climate; the majority of American fruit trees do not thrive in England, and so

forth. Many races are no good except in small districts, and sometimes even on single farms. Each race has its own taste in the matter of soil and manure, and we can only count on the expected harvest when this taste is satisfied. They behave in just the same way as the local races of our wild flowers.

9. *Natural Selection in the Field.* Much too little attention is usually paid by the biologist to this phenomenon although it is of such tremendous practical importance. Cold, frost, moisture, crowding together and late ripening select as effectively in the field as the most vigilant husbandman. Sometimes they cooperate with him but generally they are opposed to him. In the case of acclimatization they are usually on the same side inasmuch as the new climate only spares those individuals which can stand it. And the same is true of the effort to keep up old-established races of any particular country. In the cultivation of the better sorts and in empirical selection the work of the breeder might well be said to consist simply in suspending the action of natural selection. If nature and art have equal weight in the balance the value of the race does not change. In methodical selection of improved races nature almost always works against the breeder by favoring the stronger and coarser individuals. The breeder's task is therefore first to maintain his race and then to improve it.

§ 14. THE BEHAVIOR OF IMPROVED RACES AFTER THE CESSATION OF SELECTION.

As soon as selection ceases the qualities of an improved race disappear. That which has been attained by the work of many years may disappear in a few generations. The most experienced breeders express the

opinion that selection must not be neglected even in a single generation. Moreover whatever principle of selection is adopted, must be adhered to throughout if anything is to be attained.

Only a few years are necessary for a complete retrogression. And no amount of selection can prevent this retrogression or even diminish its influence. The breeder, with infinite labor and patience, and working with a large number of individuals, fixes his attention on, and improves a certain set of characters. Then nature comes, lays her hands on all the features of the race and eliminates those which even in the slightest degree reduce the strength of the plant.

"The more a race has been improved the less will it bear a cessation of selection," says Von Rümker at the end of his instructive discussion of this difficult problem.[1] Continued selection by no means fixes the character chosen, but, by separating the race further from the type from which it sprang, continually adds to the risk of regression. The maintenance of an improvement depends on the continuation of selection; for nature is continually striving to reduce the new mean to the original one. This mean is a state of equilibrium from which skilful practice can only temporarily raise the characters of a plant.

There are certain experiments on the reversal of selection which are worthy of our attention.

Peas which have been cultivated for many years on a warm dry soil regularly ripen their seeds in a short time—often about forty days; but if they are sown in another soil they preserve their property of early ripen-

[1] Von Rümker, *Anleitung zur Getreidezüchtung*, 1889, p. 81. See also Lindley, *Theory of Horticulture*, 1840, p. 314.

ing for the first year only, but in succeeding years become later and later.[1]

Then there is the well-known case of BUCKMAN who by reversing selection for a few generations converted the cultivated parsnip into the wild form (*Pastinaca sativa*). WATSON obtained the same result with the Scottish cabbage in three generations. DARWIN's verdict on this point is that a period of selection which need not extend over many generations would be sufficient to convert most of our cultivated plants into wild or nearly wild forms.

I have already mentioned SCHÜBELER's experiments on the extension of the northern limit of the culture of cereals in Norway. He found that if he took the forms which have been grown at the northern limit—that is, the short lived forms—back to their native place after a few years, that they ripened earlier and bore heavier seeds than those forms of the same sort which had remained there all the time; but that after a few generations this distinction vanished.

Fruit trees grown from seed quickly revert to the original type; the Olive to the Oleaster; apples and pears give smaller and less juicy fruit; and chestnuts become quite unpalatable.[2] But our information on these phenomena is far too meagre.

If it was not a so-called species but a subspecies which was subjected to improvement, the new form returns, on cessation of selection, not to that of the species, but to the mean of the subspecies. Double balsams and buttercups tend to become single. *Triticum compositum turgidum* (Fig. 26) becomes less branched, the

[1] DARWIN, *Das Variiren*, II. p. 42.

[2] DE CANDOLLE, *Origine des Plantes cultivées*, p. 372.

cockscombs, *Celosia cristata,* become much less flattened; but the doubling, branching and fasciation are never entirely lost and if single individuals should seem to lack them, they will always reappear in plants grown from their seed. The same conditions obtain in my experiments with *Papaver somniferum polycephalum* and in *Trifolium pratense quinquefolium.* On the cessation of selection these plants lose the high pitch of their improvement but not the character itself.

Fig. 26. *Triticum turgidum compositum,* branched Wonder or Smyrna Wheat.

I have already referred (pp. 72-73, Figs. 17 and 18) to my experiment with maize. Starting in 1886 with an ordinary race of maize whose average number of rows varied between 12 and 14, I had succeeded by 1891 in raising a race with a mean of 20 rows, a number which the original hardly ever reached. From 1892-6 the race was maintained by selection at about the same level. During the period 1897-1899 however I selected the ears with the smallest number of rows. In 1897 I sowed the seeds of a 16-rowed ear, but the mean of the harvest which they bore lay still at 20. The next year, 1898, the mean lay at 18, and in 1899 at 14-16

rows. In three years therefore the effect of the previous selection had disappeared.

The Progeny of the Original Seed. It is this retrogression which attends the cessation of selection which is, as we have already said, the chief difference between highly improved agricultural races and the so-called varieties or subspecies. The rational farmer buys his seed from that source in which it has been brought to the highest pitch of productiveness, whether this has happened by empirical or methodical selection or by particularly favorable conditions of climate and soil which act as a kind of natural selection. Such stock seed is of course dear. In the case of cereals and particularly in the case of flax, the custom is therefore to sow the bought seed and to use the harvest thus raised for the main crop; some of which may again be used for seed.[1] But the race does not retain its good qualities longer than two generations; and in order to have a satisfactory harvest it is necessary to replenish the stock seed from time to time.

We see therefore that original seed and its progeny can be wholly different in their yield.[2] And the difference is great in proportion as the conditions of cultivation are dissimilar and in proportion to the number of generations grown from the same lot of bought seed. In the first year the race retains its good qualities, but as soon as the conditions of life become different or the care spent in choosing seed for next year becomes less than that exercised previously, the good qualities of the race begin to disappear.

Change of Seed is a practice largely carried on in

[1] Langethal, *Landwirthschaftliche Pflanzenkunde.*

[2] Von Rümker, *Der wirthschaftliche Mehrwerth, loc. cit.*, p. 136.

agriculture and horticulture. There is a great deal of uncertainty as to its meaning; but it probably serves different objects in different places.

In the best known cases however this process is connected with the practice of home growing which we have just been considering. The small farmer and the gardener effect this change by making it a practice not to save seed which they have themselves harvested but to buy pedigree seed afresh. This custom is a very old one. For example MUNTING said as long ago as 1671[1] that the home-grown seed of cauliflower and savoys gave inferior results; and that seed ought to be procured afresh from Italian sources. JORDAN often sowed vegetable seeds with the object of seeing them degenerate, and regularly observed a speedy retrogression to the wild type.[2] LINDLEY states, in his *Theory of Horticulture,* cited above, that prominent seedsmen buy the seeds for the early strains of their annuals from warmer and drier districts.

RISLER says on this point[3]: "If a farmer tries to grow varieties of wheat which do very well elsewhere but are new to him and to his district he is doing the reverse of selection." Varieties are adapted to the soil and to the climate of their original home. If they are introduced in due time we may expect to reap the reward of the labor that has been spent in their perfection; but they will not last indefinitely if the conditions in which they are grown are not at least tolerably similar to those from which they came.

In 1894, J. H. VAN MANSHOLT, one of the most

[1] ABRAHAM MUNTING, *Waare Oeffeninge der Planten,* p. 319.

[2] *Arbres fruitiers,* 1853, p. 57.

[3] *Weizenbau,* p. 79.

prominent breeders in the Netherlands, has written an account of this practice as followed in his country. There are certain districts in which particular kinds of cereals retain their valuable characters unimpaired and from these other less fortunate districts obtain their seed. For example the Zeeland wheat only retains its beautiful white color in Zeeland; in Groningen and Friesland this character is lost in a few generations. Flax seeds are obtained from Riga and only quite exceptionally can they be grown without renewal for more than three or four years; for degeneration soon sets in, especially in respect of resistance to disease. A whole list of further examples leads us to the conclusion that repeated purchase of new seed stock from better localities is absolutely indispensable in the less favored districts.

The so-called process of "Intermediate Generations" is adopted in the case of the sugar beet especially. One or at most two generations are interpolated between the harvest of the seeds of polarized beets and the seed for sale. The object is to cover the cost—which is very high—of the polarization process and of selection, by vastly increasing the amount of seed for sale.

The more drastically selection is carried out the smaller does the number of select beets become and, consequently, also the amount of seed that can be obtained from them. It is necessary therefore to increase the quantity of seed, and, moreover, to do this in short time in order to reduce the amount of degeneration, due to the interpolation of many generations, to a minimum. A very curious method is adopted to effect this. The seed plants are not sown the usual distance apart but so close that the beets are only as thick as one's finger. The result of this is that the stem is only slightly branched

and ripens only the best seeds; for the seeds which are borne on the weaker lateral branches with which normal beet plants are covered are well known to be poorer. This method results in a far more stringent selection of seeds than can be effected by means of sieves or centrifugal machines; and it seems that this selection wholly or almost wholly counteracts the ill effects of degeneration resulting from the cessation of selection.

Intermediate generations are often indispensable, especially in the case of cereals. For it is obvious that in races in which the pedigree stock is small, but for which the demand is great, an enormous increase in the amount of seed must be brought about before the seed can be put on the market. But no race will stand more than 2 or at most 3 intermediate generations. Moreover if this process is not carried out with the greatest care the value of the race is lost.

Conclusion. The instability of races is the central fact on which all agricultural breeding processes are based. The seed on the market is always inferior to pedigree seed, if not in the first generation, at any rate regularly in the second or third. And no matter how long selection is carried on it cannot remove this inferiority.

IV. CONTROVERSIAL QUESTIONS.

§ 15. ACQUIRED CHARACTERS AND VARIATIONS CAUSED BY NUTRITION.

It is not my intention to enter into a discussion of the much disputed question of the inheritance of acquired characters. I only wish to show how a clear understanding of the difference between the theory of selection and the theory of mutation to a great extent simplifies, and may perhaps even lead to a satisfactory solution of, this problem.

The point at issue is really one of definition. Each author's conclusion on this question depends on the definition of "acquired" with which he starts.

Starting as we can, after the discussion in the last chapter, with an insight into the nature of selection and of improved races, let us formulate as clearly as possible what the question for decision really is.

Mutations obviously do not fall within the category of acquired characters. There can, it seems to me, be no doubt about this. They appear suddenly; we can as yet assign no cause for them; they seem independent of the environment. They are germinal variations in the strictest sense of the term.

According to the mutation hypothesis species have arisen by such mutations. Therefore specific characters are never "acquired"; and there is therefore no need for

taking "acquired characters" into consideration in the whole domain of comparative biology and the theory of descent.

The study of these characters falls within the province of variability in the restricted sense—in that of individual or fluctuating variability. It lies within the limits of the species themselves even when these limits are so narrow that they serve merely to separate the elementary species from one another.

But within these limits there is heredity.[1] The family character, the improved races of the breeder and the few scientific experiments in selection that exist prove this up to the hilt.

Are these variations brought about by external or internal causes? PLOETZ says, "the causes must of course be sought ultimately in external influences."[2] The biometrician finds it simpler to suppose that it is independent of the environment and is not causally connected with any alteration in the external conditions of life.[3] But such an assumption is obviously only a preliminary step, made only to insure simplicity in the treatment of the phenomena investigated.

There is much evidence to show that individual variations are occasioned by external influences. And if this is so we should be justified in regarding individual variations as acquired qualities. For most authors call those

[1] We are not taking here into consideration the question of the inheritance of the effects of wounds and mutilations. They are inherited *perhaps exclusively when followed by disease* as DARWIN said (*Variation,* II, p. 57), that is by infection.

[2] ALFRED PLOETZ, *Die Tüchtigkeit unserer Rasse und der Schutz der Schwachen,* 1895, p. 32. See also p. 23. Also *Intracellulare Pangenesis,* p. 29.

[3] G. DUNCKER, *Die Methode der Variationsstatistik.* ROUX's *Archiv f. Entwick. Mech. d. Org.,* Vol. VIII, 1, p. 115, (1899).

characters "acquired" which can be traced to some effect of the environment on the organism in question.[1]

Acquired characters, as the term is understood in Zoology and Anthropology, are parallel to the so-called nutritional modifications of the botanist.

Let us compare the two groups of phenomena.

We often find in the literature of this subject a distinction drawn between the so-called nutritional characters and individual variations. The former are said not to be heritable and therefore not to provide material for selection. But the latter are assumed to be due to unknown causes, and to be heritable and fixable by selection.

The phenomena of nutritional modifications are equally well known in agriculture and in horticulture. The edges of the field and the spots in it which have received an undue share of manure give rise to luxuriant plants. On the other hand the weed that germinates in mid-summer is often of shrunken stature and after producing a few leaves, blooms and sets seed. In the garden too, plants which are grown in dry places or in poor soil or which come up late are often miserable specimens. We often see beside richly branched *Datura*, beside *Amarantus* a meter high, beside normal buckwheat or a poppy covered with blossoms, single specimens often only a decimeter high, almost or quite unbranched, with small and few flowers which nevertheless are able to set seed though these may be few in number.

If we seek for the grounds on which the distinction so often drawn between nutritional modifications and in-

[1] Other types of definition, especially those which involve the question as to whether the variations arise in the germ or not lead to much confusion. See *Intracellulare Pangenesis*, p. 206, and *Kruidkundig Jaarboek*, Vol. I, 1889, p. 152.

dividual variations is based, we seldom find them clearly stated. And when we can, they usually consist in some misapprehension of the meaning of the term Heredity. Nutritional modifications are deviations of considerable magnitude, which are soon lost in succeeding generations in accordance with the law of regression. They do indeed bear a certain resemblance to spontaneous variations or sports which are of course inherited. It is perhaps on some such train of thought as this that the view that they are not inherited may rest.

Ordinary variation evidently must be due to some cause and this must be sought for, in the last instance, in the environment: that is in nutrition, using that term in its widest signification.

My experiments lead me to the conclusion that nutritional modifications and ordinary variations are one and the same thing. Great changes in nutrition result in great changes in the plant followed by a proportionately speedy regression. And as the change in the organism does not become independent of nutrition, a change in the amount of manure in the next generation will affect the plant accordingly.

Nutrition in the widest sense—the conditions of life one might almost say—is at the bottom of all individual variability.[1] Every character varies only in a *plus* or *minus* direction. Favorable conditions are responsible for the former, unfavorable ones for the latter. Which particular influences are favorable and which are not, is of no importance; in the words of KNIGHT: "Superfluity of nutriment is the most important cause of variability: the kind of nutriment does not matter," he said. Future

[1] *L'Unité dans la variation*; Revue de l'Université de Bruxelles, III, 1898.

investigation may succeed in isolating the individual factors of the environment as they affect the organism, but at present we must be content with treating them together, as one phenomenon.

It is simply impossible to draw any distinction between these nutritional modifications and individual variations in the strictest sense of the term. There seems to be every stage in the transition from a state of affairs in which the effect of external conditions is easily traceable as in the case of nutritional modifications, to one in which the very reverse is the case. But this condition of things is only apparent, for the more closely we go into the matter the more evident does it become that the changes of this kind (individual variations) are correlated with changes in the environment.

In horticulture it is well known that favorable and highly altered conditions lead to the accumulation and multiplication of individual differences whilst ordinary and uniform conditions tend to dissipate them and to reduce all the individuals to the same level.[1]

It is also well known that weedy specimens by no means lack the characters of the variety to which they belong but that they are simply *minus*-variants in fluctuating variability.

More accurate investigation will, doubtless, bring out the identity of true individual variations with nutritional modifications. Mac Leod has conducted some very instructive experiments in this connection. He compared the number of marginal florets on well-grown and starved specimens of the common cornflower (*Centaurea Cyanus*) and found that there was a very high positive correlation between number and vigor. The stronger the plant the

[1] *Intracellulare Pangenesis,* p. 30.

richer are its inflorescences in marginal florets. But the luxuriance of the plant is the direct result of nutrition, and we cannot escape the conclusion that the same is true of the marginal florets. And the same rule applies to the whole organization of the plant.[1]

Our conclusion is therefore that we have two categories of characters, one which includes mutations only; and another which includes "acquired characters," nutritional modifications and individual variations. The only difference between true individual variations and these modifications is that the latter are determined in a more evident manner by external conditions.

§ 16. ON THE INHERITANCE OF ACQUIRED CHARACTERS.

Herbert Spencer is more than any one else responsible for the doctrine of acquired characters.[2] He starts with the belief, based on general observation, that the differences between the individuals of a species are caused by the conditions in which they live and that such differences are inherited.

We have seen in the preceding sections how acquired characters manifest themselves as individual deviations from the mean character of the type in question. The question of their inheritance must therefore be judged from this point of view.

The inheritance of individual variations differs from that of mutations in that the former exhibits the phenomena of regression and of accumulation by selection.

[1] J. Mac Leod, *Over de veranderlykheid van het aantal randbloemen by de Korenbloem.* Handelingen Vlaamsch Natuurk. Congres, 1899.

[2] See especially his various essays in *The Contemporary Review.*

Mutations are inherited and, as a rule, constant from the time when they appear. Reversions to the parent form are not wanting; but they are very rare and take place as sports and not by a series of transitional forms. We call this atavism.

The inheritance of variations or deviations from the mean of the type is quite a different thing. The children deviate less, on the average, from the mean than the parents do; on the other hand some individuals of them may differ more, and these enable us to increase the deviation by means of selection.

The answer to the question whether acquired characters are inherited, is that they are not so in their entirety, but with a reduction the amount of which is indicated by GALTON's law. On the other hand the gradual change in the mean character of a race which can be effected by selection is sufficient proof that these characters really are inherited. The question whether such variations are inherited becomes the question whether they can be increased by selection. And as far as I am aware no investigations have been made which prove that this cannot be done.

The so-called innate characters as opposed to acquired ones are believed to be inherited while the latter are not; but it is obvious that they are merely inherited deviations from the mean, and that the ancestors, which showed these deviations must have acquired them themselves under the influence of external conditions. It would lead us too far to follow up this line of thought although such a discussion would undoubtedly contribute to the ultimate solution of this question.

If we regard individual variations as brought about by environment and by nutrition in the widest sense,

we arrive at the conclusion that selection consists in the choice of the most highly nourished.[1] Nutrition can obviously not effect the full amount of change to which it may lead, in a single generation. Seeds ripen on the mother-plant; and in the ripening seed the young plant passes a very important and, what is still more important, a very sensitive portion of its life-history. At this period it is obviously dependent on the nutritional conditions of the mother. If the mother-plant is not strong—and not grown itself from strong seed—it cannot give rise to the strongest offspring. It takes, therefore, a few generations for the surrounding conditions to exert their full effect. And as variations are caused by nutrition, so it must be possible to increase them by selection of the best nourished individuals within some few generations.[2]

It has been my object in this discussion to offer a solution of the question of the inheritance of acquired characters by a critical analysis of the theory of selection. A solution on some such lines as those suggested may moreover lead us to the only path that will help us —that of experimental investigation. Once on this path the first thing we have to do is to find out whether variations which are to a great extent dependent on environment can be intensified or diminished by selection in the ordinary way.

In conclusion, seeing that the material proof is meagre, we may illustrate this by the case of polycephaly in *Papaver somniferum*.[3]

[1] It seems not unreasonable to regard the effects of use as due to the increased nourishment of an organ.

[2] *L'Unité dans la variation*, pp. 21-22. (Revue de l'Université de Bruxelles, Tome III, 1898, Avril.

[3] *Alimentation et sélection.* Volume jubilaire de la Société de Biologie. Paris 27 Déc. 1899, p. 17. Ref. in Biolog. Centralblatt, Bd. XX, No. 6, 1900.

This species is said to be highly variable; but all that is meant by this is that it is very rich in subspecies. One of these is distinguished by the conversion of the inner stamens into carpels. It is cultivated in many of our gardens under the name of *P. s. monstruosum* or *P. s. polycephalum* (Fig. 27). It is, according to my observations always true to its type but is highly variable (Fig. 28). The number of supernumerary carpels may reach 150 or more; or they may be reduced to mere rudiments: though, so far as my experience goes, they are never entirely lacking.

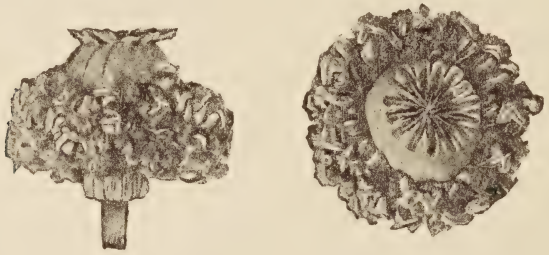


Fig. 27. *Papaver somniferum polycephalum s. monstrosum,* with a whole wreath of supplementary carpels. From above and from the side.

The variability of the character in question is almost entirely dependent on the conditions of life. From the seeds of fruits with a beautiful circlet of carpels we can raise a good harvest of such; or a bad one, just as we please. The more favorable the conditions the more numerous the supernumerary carpels.

It is evident that it is impossible to make the conditions for each plant in a bed exactly similar, for when the seed first begins to germinate there are differences in illumination, humidity, supply of nutriment, etc., whose influences tend, as growth proceeds, not to level up the differences, but, on the contrary, to accentuate them. In

experiments, therefore, only the mean characters of different beds may be compared. In doing so, we find as a general rule that good soil, heavy manuring, a sunny position, evenly distributed moisture and, above all, plenty of room between the plants, tend to increase the number of carpels per flower; whilst sandy soil, shade, cold,

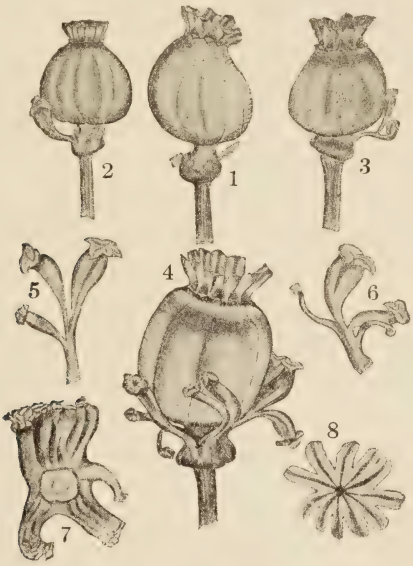


Fig. 28. *Papaver somniferum polycephalum,* with slight multiplication of carpels. 1 with rudimentary carpels; 2-4 with 1, 2 or a few such; 5, 6 and 7, various stages in the fusion of the lateral fruits which in 7 have fused to a split wreath round the central capsule (which has been removed). 8, stigma of the central fruit seen from above.

drought and crowding of the plants decrease the number to a very considerable extent; indeed the strongest plants bear a full "crown," the feeblest scarcely any trace of the monstrosity.

In the process of looking for the best plants for experiment I soon noticed that the individual strength of

the plant is highly correlated with the number of supernumerary carpels. The thickness of the stem, the height of the plant, but especially the weight of the fruit afford a good index of strength. If we arrange the individual plants of a bed, in a row according to this latter character, we find that they form an almost regularly ascending series with regard to the monstrosity.

It follows therefore that a selection with reference to the elaboration of the carpellary crown is by no manner of means without relation to the general nutritional condition of the plant. On the contrary such a selection is merely a selection of the most highly nourished.

It is just the same if we deal with the *minus*-variations. It is only the feeblest specimens which are destitute of fully developed supernumerary carpels though as we have said they possess 1 or 2 rudimentary ones; their capsules are often so small that they do not contain good seed. If we look for capsules with better seeds we find more pronounced traces of the monstrosity. Retrograde selection or selection in a *minus* direction obviously consists therefore in a choice of the weakest individuals.

Nevertheless, in both these cases selection has the effect that it usually has. From the seeds of self-fertilized plants with a very large number of metamorphosed stamens we get offspring with this character highly developed; from seeds from fruits poor in supernumerary carpels, a race exhibiting this monstrosity only to a very slight extent. Continued selection for a few generations intensifies this effect, provided that the conditions under which the plants were grown are average ones and that the experiments are carried out on a large scale extending over several square meters of ground.

External conditions, then, exert corresponding in-

fluence on the monstrosity whether we have regard to the carpels themselves or to the seed which they contain. In the experiments in question their operation begins with the germination of the seeds which are to produce the plants for the experiment. The degree of development of the monstrosity in such cases would be called an acquired character in the usual acceptance of the term. There is no obvious reason why we should not apply this term to the improved value of the seeds obtained in this experiment—an improvement that has been brought about by the very same external conditions which affected the monstrosity.

The parallel between individual strength and the development of the monstrosity is not absolute. On the contrary there is a very simple means of separating the two and of obtaining plants of great vigor but almost destitute of supernumerary carpels. This process rests on an accurate determination of what we may call the impressionable period in the development of the monstrosity. If we examine the young buds under the microscope at intervals, we find at about the sixth week from the germination of the seed the stamens and supernumerary carpels represented by small protuberances on the growing summit. The relative number of the two structures is obviously settled at this stage; all attempts to alter their relative proportions by subjecting them to different conditions, after this stage has been reached, have been without avail. The critical stage occurs, then, during the first few weeks of life; so that it is during this period alone, if ever, that it should be possible to suppress or at any rate to reduce the monstrosity. I have succeeded in doing this, simply by transplanting the young seedlings at the proper time, that is when they

have 2 or 3 leaves in addition to the cotyledons. If, after that, I make the conditions as favorable as possible, I get large and vigorous plants with but few stamens transformed into carpels.

By this device therefore it is possible to separate the two acquired characters, previously associated. The acquisition of the visible monstrosity is prevented; but the seeds attain their full development.

Parallel experiments with other species and other characters have convinced me that we are dealing in this case with a universal and very important principle. I mean the simultaneous influence of the conditions of life on the visible character of an organism and on its germ cells. In other words (using the word nutrition in its old broad sense) we may say that *selection is the choice of the best nourished individuals.*

This statement can only be taken in a very general sense; for there are individual cases to which it does not seem to apply, as for instance the case of the selection of *minus*-variations. Moreover in other cases there are special circumstances which prevent its exact application, for example in agricultural selection where the plants have to be adapted to a supply of manure which can never be copious.[1]

We are thus led to see that a proper understanding of the difference between the theories of Selection and Mutation opens up the possibility of a solution of the question of the inheritance of acquired characters. Specific characters are excluded once and for all from this discussion; they arise suddenly by mutation and are not acquired. Individual deviations from the mean of the specific character are to be regarded as acquired char-

[1] On this point see the previous chapter especially § 12.

acters; they depend, as far as our scanty information goes, almost entirely on external conditions; which in their turn, however, need some generations in order to exert their full effect.

The only way to decide this point is to carry out extensive and numerous experiments in selection, dealing with the general significance of nutrition in its widest sense.

§ 17. ON PARTIAL VARIABILITY AND SELECTION BY VEGETATIVE METHODS OF PROPAGATION.

Partial variability, that is, differences in homologous organs of the same individual, plays a much more important part in the vegetable than in the animal kingdom. It is as universal as the differences between individuals and is usually more pronounced.

It conforms to exactly the same statistical laws. The size of leaves, of flowers and of fruits, the number of leaves on a branch and of the parts of the flower, the rays in the inflorescences of Umbelliferae and Compositae even if determined on a single plant can be tabulated by means of frequency curves. The phenomenon of regression in partial variability has been made the subject of special study by VERSCHAFFELT: and the laws describing it were found to be the same as those formulated by GALTON for individual variability.[1] Lastly, the principles of selection apply to these phenomena as well as to individual variability.[2]

This great similarity between individual and partial

[1] ED. VERSCHAFFELT, GALTON's *"Regression to mediocrity"* by ongeslachtelyke Voortplanting. Livre jubilaire dédié à CHARLES VAN BAMBEKE, Bruxelles, 1899.

[2] See the end of this section.

variability serves to place the antithesis between mutability and individual variability in an even stronger light.

I shall therefore briefly touch on a few examples of partial variability.

One of the most valuable pieces of work in biology are STAHL's classical researches on the effect of sunny and shady positions on the development of foliage leaves.[1] The insolated leaves are generally smaller, stouter, poorer in air spaces and richer in chlorophyll and have stronger veins; they are in fact adapted to turn the strong sunlight to best account. The shaded leaves are broader and thinner, with larger air spaces and delicate epidermis—in fact eminently adapted to make the most of the meagre supply of light at their disposal. *Lactuca, Iris, Fagus* are the best known examples. The more a species has become specialized as a "sun-plant" as *Pinus*, or a "shade-plant" as *Chelidonium*, the less is its power of adaptation in this direction.

Still more important, if possible, than STAHL's researches are GASTON BONNIER's recent investigations on the adaptation of plants to arctic and alpine climates.[2] Both authors dealt with partial variability; the former dealing with the problem from a comparative standpoint, the latter from an experimental one. In BONNIER's experiments a single individual of each species that was dealt with was divided into two. One of the parts was then grown on the Alps or Pyrenees; the other on low lying land. In the course of a very short time the former

[1] *Jenaische Zeitschrift für Naturw.*, XVI, N. F., IX, 1, 2, 1883.

[2] G. BONNIER, *Recherches expérimentales sur l'adaptation des plantes au climat alpin.* Ann. Sci. nat. 7. Serie, T. 20. *Les plantes arctiques comparées aux mêmes espèces des Alpes et des Pyrénées.* Revue générale de Botanique, Tome 6; *Influence de la lumière électrique sur la forme et la structure des plantes.* Ibid., T. 7, 1896.

half took on the familiar dwarf habit of alpine plants while the latter soon exhibited the general features of lowland plants. The leaves of alpine plants are smaller, thicker, firmer and more compact in build, poorer in air spaces, richer in chlorophyll and dark green; in a given period of time they assimilate more carbonic acid gas than the corresponding parts of plants grown in the plain. They are perfectly adapted to the bright light and the short summer of the Alps; in the space of a few weeks they have to store up nourishment for the whole year. The underground stem of an alpine plant is well developed and richly branched; the exposed parts are on the other hand short and consist of few and stunted internodes; it has large flowers and so forth. In all these respects the half-specimens transplanted to the Alps assumed the characters of normal alpine plants.

Arctic plants exhibit a corresponding adaptation; the climate is of course cold, but the air is damp, and this affects the anatomical structure of the leaves. This case of partial variability has also been investigated by Bonnier, and with analogous results.

I have carried out similar experiments, on a Crassula-like composite *Othonna crassifolia*.[1] It is a South African plant with almost cylindrical fleshy leaves pointed at the end. The development of these leaves is to a great extent dependent on the dampness of the air and the ground. Grown in damp soil, the *Othonna* is dark green, with long leaves, it is richly branched and of very luxuriant growth; grown in dry soil on the other hand it is very pale green, with short globose leaves, and hardly branched at all. They also exhibit a dependence on external conditions in the number of their ray-florets, a

[1] *Kruidk. Jaarboek Dodonaea.* Bd. XII, 1900, Taf. 1.

character which has so often afforded material for statistical investigation. Their variation can be expressed in the form of curves; the mean for dark green individuals which have been liberally watered stands at 13 ray-florets, but for a separate part of the same plant which had been kept relatively dry the mean was 12.

Fig. 29. *Helianthemum vulgare* after G. Bonnier (*loc. cit.*, Plate 20). The plant was divided in two halves of which one (*a*) was subsequently cultivated in the plain and the other (*b*) in the Alps. Both halves are reduced on the same scale in the figure.

In these instances nutritional modifications are seen to be adaptive characters; in one case these adaptive differences are what we should describe as instances of normal variability; and they are obviously brought about

by the same causes. This alone would suffice to show how intimately the two phenomena are connected.

A further fact, to which much too little attention has been paid, is the gradual accumulation of some peculiarity by means of selection of a character in a plant propagated

Figs. 30 and 31.

Othonna carnosa, I*a* grown in moist earth and I*b* in dry; the former with long leaves forming no rosettes and very strong; the latter covered with rosettes of short stout thick leaves.[1]

Othonna crassifolia. II*a* grown in damp soil and II*b* in dry, II*c* a flower. I*b* and II*b* were branches hanging over the edge of the pot.

by vegetative methods. An example of this has been given by DARWIN:[2]

The well-known English plant-breeder SALTER effected a considerable improvement in certain variegated

[1] *Othonna carnosa* is very like *O. crassifolia,* but has considerably larger leaves and somewhat larger flowers. But its relation to damp air and so forth is the same as that of *O. crassifolia.*

[2] *Variations of Animals and Plants,* I, p. 443, 444.

plants by carefully selecting the twigs which were to be used as cuttings. His plan was to look over a plant for any leaves which showed even the slightest indication of variegation and then to make cuttings from the buds in the axils of these leaves. The leaves gave the promise of a higher degree of variegation, and justified it by enabling SALTER to put several varieties on the market.

The same principle has recently been applied with the most satisfactory results by J. KOBUS in the cultivation of sugar cane in Java.[1] There are great difficulties in the way of propagating the selected plants sexually in this case, the most serious of which is that the best kind of all—the Cheribon cane—is sterile. KOBUS, therefore, sought among the best varieties that which was richest in sugar and only used this to take cuttings from (such cuttings are called *bibit* in Java). But all the specimens of a single variety are, in this case, obtained by vegetative methods, so that every variety is, as we have explained above (pp. 84-85) a single individual. The cuttings from individuals rich in sugar give rise to rich canes. This method insures, in the first place, the elimination of the less valuable plants in a very simple and effective manner, and in the second, the use of the very best canes as breeding material: moreover the yield is much more quickly and much more simply increased than by the ordinary method of selection.

To sum up: I claim that I have shown that there is a complete parallel between partial and individual variability; and that both are brought about by the same causes. These are external; they are to be found in the amount of light and of moisture and in such other factors as would be placed in the category of "nutritional"

[1] *Archief voor Java-Suikerindustrie*, 1898, Nr. 16, 1899, Nr. 15-16.

—according to the old acceptance of the term nutrition. Their effect can be intensified, in the case of partial as well as in that of individual variability, in the course of a few generations whether these be sexually or vegetatively produced.

§ 18. VARIATION AND ADAPTATION.

It has often been maintained that groups of individuals which vary are better adapted to a changing environment than groups of individuals which are all alike.

Variability must not, however, in my opinion be regarded solely as an adaptation. But the fact that the amplitude of variation, the *Abänderungsspielraum* as AMMON has happily termed it,[1] is very different in different organs and characters and also in different species of animals and plants suggests that there must be a definite cause for it in each particular case.

The form of a QUETELET's curve is determined by two factors; the magnitude of the mean value and the amplitude of variation. We are accustomed to regard as a measure of the latter that part on the base line which includes half of the individuals between the mean and the furthest scale character. The mean (M) and the amplitude (Q) are independent values. But they are both specific characters at least in every case in which they deviate from the normal. And it is not necessary to say here that specific characters are at least in very many instances adaptive characters.

I shall now examine two very important phenomena from this point of view. First, the frequently enormous

[1] OTTO AMMON, *Der Abänderungsspielraum.* Naturwissensch. Wochenschrift, 1896, Nos. 12-14.

variability of vegetative organs and the equally remarkable uniformity of organs connected with reproduction; and further the dissimilarity between seeds on one and the same plant.

Vegetative organs are as a rule much more variable than those which are concerned with sexual processes. The characters of flowers exhibit very slight variability: and the more they are adapted to the visits of insects the less variable are they. The number of petals and stamens is remarkably constant so long as the number is small; but when their number becomes so great that a few more or less would exert no perceptible influence on the shape of the flower, it ceases to be constant. The symmetry of the flower is hardly subject to variation at all. The more exactly a flower is adapted to the visits of single genera or species of insects the more serious would any deviation from the normal form be; and we do as a matter of fact find that in such cases deviations are exceedingly minute and rare. On the other hand when we consider the vegetative life of a plant we see that it is of the highest importance that the plant should be able to make the most of the amount of light, moisture, inorganic food, and space at its disposal, that is, to be in a position to develop luxuriantly in favorable circumstances and economically in unfavorable ones.

There is a whole series of plants which are remarkable for an extraordinary plasticity of this kind. It is often assumed that the general conditions affecting the growth of a plant on such a small area as a garden bed are in themselves uniform or at any rate that they can be easily made so. But my experience, which is derived from such experiments extending over more than ten years, has convinced me that the difficulties in the way of

insuring such uniformity are almost insuperable. And if these differences cannot be removed in our experiments it is obvious that the effect they have in nature must be considerable. So that a sowing of dissimilar seeds in nature gives more promise of a strong generation than a sowing of similar seeds. For the conditions obtaining in the different parts of a circumscribed area, as far as they affect the germination and growth of a seed are very different, partly on account of differences in dampness and fertility—which varies inversely with the degree of exhaustion of the soil—partly on account of enemies in the shape of animals and partly on account of competitors in the shape of plants between which they happen to be lodged. But if the number of seeds is great and the differences between them are considerable, there is every likelihood that at any rate some of them will find a situation which suits them.

Let us take a particular case and compare the variability which exists in nature with that which is exhibited by a population produced by sowing the seeds of a single plant. I have chosen as an example the yellow cornflower of our fields (*Chrysanthemum segetum*) and have paid attention to the number of ray-florets on the inflorescence.[1] The average number of these is 13; but the plants vary round this value in the one direction to 6, in the other to 21.

Dr. H. W. Heinsius has been kind enough to make some observations for me in the field in North Brabant in the Netherlands; they involved the counting of ray-florets on 325 flowers. In 1894 I sowed the seeds of a 13-rayed plant and counted the ray-florets of the first

[1] *Ueber Curvenselection bei Chrysanthemum segetum,* Berichte d. d. Bot. Ges., 1899, XVII, pp. 87-89. The numbers given there are here reckoned as percentages.

flower on every plant in the population obtained. There were 338 plants. Both series of numbers are transmuted into percentages to make their comparison simpler. Here is the result:

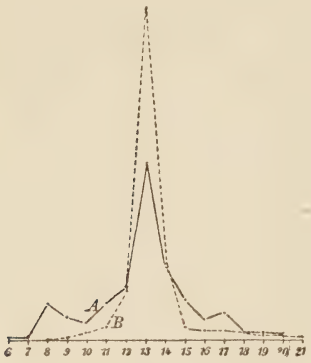


Fig. 32. Curves of large and small amplitude. A, curve of the variability of the number of ray-florets of *Chrysanthemum segetum* growing wild. B, the same curve describing a crop obtained in 1894 by sowing the seeds of a 13-rayed plant. The numbers at the feet of the ordinates correspond to the number of ray-florets in the inflorescence.

NUMBER OF RAYS	IN THE OPEN	AFTER SELECTION
6	0.3	0.0
7	0.3	0.0
8	6.8	0.0
9	4.3	0.3
10	3.1	0.9
11	7.1	2.3
12	9.9	9.3
13	34.2	65.3
14	14.2	14.8
15	8.0	2.3
16	3.7	1.5
17	5.2	1.2
18	0.9	0.9
19	0.9	0.3
20	0.9	0.6
21	0.0	0.3

In Fig. 32 these two series of figures are exhibited graphically as curves. It will be seen at once that the dotted curve which describes the result of the culture in 1894 has a much higher apex and is much steeper than the other; that is, it has a much smaller amplitude. In other words, the deviations from the mean in plants growing in the field are greater in size and number than they are among the children of a single plant, even when this plant bore exactly the mean character of the type.

It is clear that a generation corresponding to curve

A will have less difficulty in finding conditions to suit it than a less variable one, such as might be described by curve B. The offspring of seeds of varying parents are therefore at a considerable advantage.

And now we come to the significance of crossing. The essence of fertilization is not the union of the two sexes but the mixture of the heritable characters of two individuals with a different past or at any rate of individuals which have been subjected to different external conditions. The advantages accruing from the fusion of different variants afford, in my opinion, a fair explanation of the existence of sexual reproduction.[1]

DARWIN's well-known aphorism: *nature abhors perpetual self-fertilization,* does not seem to me to express the matter quite exactly. It is not sufficient that isolated crossings should occur from time to time; on the contrary, it is necessary that a certain percentage of individuals should always be crossed. For in this way variability will be increased;[2] but the point is not that its range should be as wide as possible but that it should be maintained at a limit which the environment demands.[3]

The degree of the deviation of the individual is already determined in the seed. But seeds differ among themselves not only in relation to the characters of their parents, but according to the position on the plant itself and according to their weight. The significance of these factors and their bearing on variability has often been the subject of research; numerous isolated papers on this subject exist but they need a comparative and critical

[1] *Intracellulare Pangenesis,* p. 29.

[2] A. GIARD in *Comptes rendus de la Soc. de Biologie,* 4 Nov. 1899, p. 2, and LIGNIER in *Festschrift zu Ehren Giard's,* Nov. 1899.

[3] See especially AMMON, *Der Abänderungsspielraum, loc. cit.,* p. 53.

treatment.[1] Far too little attention has been paid to the relation between the range of variation of the individual characters and the degree of their adaptation to changing conditions of life; and the whole matter is still very much of a mystery. Here again it is probable that further study will tend to emphasize the fundamental distinction between variability and mutability.

§ 19. VARIABILITY IN MAN, AND SOCIAL QUESTIONS.

A noteworthy feature of the last few decades has been the attempt to apply the results of evolutionary investigation to the solution of the great problems of humanity and social life. Many have followed along the lines which the great English philosopher HERBERT SPENCER laid down; and a considerable mass of literature has accumulated on this subject. There are at least two important schools in this field of research. OTTO AMMON is the founder of one of them: his method consisted in the application of the results of statistical investigations. The other, and much larger school, is that which aims at the application of biological, and particularly of zoological knowledge to the solution of social problems.

AMMON'S method seems to me to be justified by the fruit it has borne; but the writings of biologists in general and zoologists in particular seem to me to fall short of a desirable standard of lucidity and directness.[2]

Many mistakes may in the future be avoided if a clear distinction be drawn between mutability and variability in the ordinary sense.

[1] See VON RÜMKER, *Der wirthschaftliche Mehrwerth, loc cit.*, pp. 140-141.

[2] A general account of the methods and results of this school, and a bibliography will be found in O. HERTWIG'S essay, *Die Lehre vom Organismus und ihre Beziehung zur Sozialwissenschaft*, 1899.

The variability exhibited by man is of the fluctuating kind: whereas species arise by mutation. The two phenomena are fundamentally different.[1] The assumption that human variability bears any relation to the variation which has or is supposed to have caused the origin of species is to my mind absolutely unjustified.

Man is a permanent type, like the vast majority of species of animals and plants. The laws for permanent types apply to man; though often with a qualification. But the laws which describe the changes by which individual permanent types arise cannot be so applied. As we have seen it is characteristic of these types to exhibit a certain amount of fluctuating variability. Man is no exception to this rule.

Therefore all that we can apply to the treatment of social questions is our knowledge of ordinary variability. The facts of specific differentiation are interesting but not relevant.

The mental qualities of the human race are closely bound up with their bodily organization, and this has been shown to conform to the same laws as those by which we describe individual variability in plants and animals.

Of late years, KOLLMANN has done more than any one else to insist on the distinction which should be made between persistent racial characters and fluctuating intra-racial characters in the case of man—a distinction which was also emphatically maintained by VIRCHOW.[2]

Favorable and unfavorable conditions of life, migra-

[1] *L'Unité dans la Variation, loc. cit.*, p. 17.

[2] KOLLMANN, *Die angebliche Entstehung neuer Rassentypen* in Correspondenzblatt der d. Gesellsch. für Anthropologie, Vol. 31, No. 1, Jan. 1900, p. 1. A bibliography of the subject will be found on page 5.

tion to a different climate and so forth affect the fluctuating characters of man to no small extent. But only for a time; as soon as the disturbing factor is removed, the effect which it produced disappears. The morphological characters of the race on the other hand are not in the least affected by such influences. New varieties do not arise by this means. Since the beginning of the diluvial period man has not given rise to any new races or types. He is, in fact, immutable, albeit highly variable.

In order to attain to some insight into the causes and significance of individual differences in man we must study the corresponding differences which are presented by an assemblage of forms belonging to a single species of animal or plant. Here is a wide and fertile field open for investigation; but one in which the harvest of information has been poor so far.

Ammon, as we have already said, is the most considerable of the anthropological writers on this subject. Although he does not distinguish between the theories of selection and mutation, he sees clearly that our knowledge of the origin of species in nature has no bearing on social questions. And as it is on this point that most sociological writers are in error it will be worth our while to pay some attention to his actual position.[1]

Ammon sets forth the modern theory of selection in five theses of which the first four deal with heredity, variability, the struggle for existence and elimination of the unfit (Natürliche Auslese).[2]

The fifth thesis deals with the theory of descent. It runs: "The forms and characters which, having arisen

[1] Otto Ammon, *Die Gesellschaftsordnung und ihre natürlichen Grundlagen*, 2d edition, 1896, pp. 9-10.

[2] This happy phrase of Ammon is eminently preferable to *Natürliche Zuchtwahl.*

as the result of variability, are favorable to the survival of the individual increase in relative number by the natural elimination of unfavorable ones. New varieties and species arise by the gradual accumulation, generation by generation, of the favorable deviations from the original type.

And then he adds, "The substance of the fifth thesis is often challenged on the ground that we are not in a position to state that deviations from a certain type can lead to the origin of a new species by the elimination of the unfit. Fortunately we need not wait for the settlement of this controversy. I have only enunciated the 5th thesis in order to give a complete survey of DARWIN'S theory; *but it has no bearing whatsoever on our present socio-anthropological inquiry.*"

This is not the place in which to go further into this question. The danger of the application of the theory of descent to social questions has already been pointed out by men who are qualified to express an opinion. Quite lately KARL PEARSON has severely criticized BENJAMIN KIDD'S book on social evolution which is often recommended in England as the best up-to-date work on the subject. If the reader is not clear as to what is meant by the dangers, to which we have referred, which attend the application of the so-called scientific method to the treatment of these problems he will do well to read this critical essay carefully.[1]

So long as it is impossible to investigate the social qualities of man *directly* it must suffice to do what we can by analogy. Material for this argument is afforded by the study of variability in the stricter sense of the

[1] KARL PEARSON, *Socialism and Natural Selection,* The Fortnightly Review, 1894.

term; but our knowledge of the mode of the origin of species will not help us in this investigation.[1] The study of variability, in plants and animals, as well as in the physical characters of man may thus serve a higher purpose.

It is singularly fortunate, in the present state of affairs, that these analogies should be limited to variability as opposed to mutability. Variability is accessible to investigation from many points of view, which is far from being the case with mutability. Many principles in variability have been discovered and dealt with by QUETELET and GALTON and their followers: the methods of this school can be partly applied directly to the investigation of mental characters and partly effect a considerable simplification of treatment.

There lies here a wide and fertile field of investigation, especially for botanists.[2] One of the most important conditions in experiments on selection is the number of individuals in each generation; and plants readily lend themselves to cultivation by hundreds without any of the ill effects which usually attend overcrowding. Such experiments are well-nigh impossible in the case of animals: and out of the question in the case of man. Here, as in many other spheres, the botanist must take the lead and the zoologist and anthropologist will follow afterwards.

Of late years the statistical study of variability has become specialized as a distinct branch of science thanks to the labors of BATESON and WELDON among zoologists, LUDWIG among botanists and KARL PEARSON and DUNC-

[1] See also H. J. HAYCRAFT, *Darwinism and Race Progress*, and further, on the possibility of replacing selection by improved nutrition: *L'Unité dans la Variation*, p. 21.

[2] *L'Unité dans la Variation, loc. cit.*, pp. 14-15.

KER among mathematicians. Botanical work in this field, has also been done by VERSCHAFFELT, BURKILL, HAAKE, DAVENPORT, BLANKINSHIP, MAC LEOD and many others.[1]

Let us summarize the foregoing discussion. The mental and moral characters of men exhibit fluctuating variability. The laws therefore which describe this phenomenon can be profitably applied to such characters. And we shall have to be contented with this manner of treating the subject so long as a *direct* investigation by biometric methods, and by experiments in selection are out of the question. The foundations of sociology must be furnished by biology. And we may hope that the time is not far distant when a fruitful cooperation between these two sciences, apparently so much akin but actually so far apart, may be brought about.

But no theory of the origin of species can have any bearing at all on this subject.

§ 20. SOME SUBJECTS FOR FUTURE INVESTIGATION.

In the preceding discussion I have had occasion to draw attention not merely to the splendid achievements of my predecessors but also to the numerous gaps in our knowledge.

The study of variability as opposed to mutability is a branch of human knowledge which has developed with great rapidity in the last few years. The statistical method of dealing with this phenomenon is, as we have

[1] A survey of the literature on this subject has been given by G. DUNCKER, *Die Methode der Variationsstatistik*; ROUX'S *Archiv für Entwickelungsmechanik*, Vol. VIII, 1899, p. 167; and by OSTERHOUT, *Problems of Heredity* in Contributions Bot. Semin. Univ. California. 1898.

already said, firmly established: comparative and experimental methods are just coming on.

I propose, therefore, to suggest a series of problems the solution of which would in my opinion throw much light on the essential difference between mutability and variability.

1. More examples of QUETELET's law are wanted: their number can never become too great.

2. The curves in question should be plotted from the same individuals or from the same batch of individuals in successive years. The constancy of their means and their amplitude (GALTON's Q and Q′) should be determined. Changes in these values, and changes in the symmetry of the curves, should if possible be traced to their causes.

3. Polymorphic curves should be looked for and analysed. These may point to the existence of mixtures of perfectly distinct elementary species growing together or to the existence of antagonistic characters within the limits of a single species (for examples annual and biennial forms in *Daucus, Beta,* etc.) They may also be due to diseases. Finally they may be the so-called "double curves" in which the several apices are to be regarded as ordinates in a curve of a higher order, and not as indications of mutation.

4. Correlative variation is a phenomenon of the highest importance.[1] For example man presents many instances of correlation between mental and physical characters. Correlations fall in two categories. In the one are those cases in which the two characters are dependent in the same way although not to the same degree on ex-

[1] J. H. BURKILL, *Variation in the Number of Stamens and Carpels,* Journ. Linn. Soc. Bot., Vol. 31.

ternal conditions. In the other are those cases in which variation in one character is the cause of variation in another,[1] as for example the various phenomena of growth which are correlated with differences in photosynthetic activity. It is superfluous to refer the reader to GALTON's method of studying correlation.[2]

5. The relation between external conditions of life and variability ought to be investigated. Are there variations which are independent of such, or are there not? If there are, what are their causes? Do the individual external factors exert a separate influence or not? Is there a definite relation between the extent of this influence and the magnitude of the variation? Do all characters under the influence of high nutrition vary in a *plus* direction, and under a poor one in a *minus* direction?[3]

6. The sensitive period in the development of characters should be determined. When the rudiments of organs are visible under the microscope it is usually too late to exert any restraining influence on their development. But there may be exceptions to this rule. During the time which a character takes to develop there is probably one short period of extreme susceptibility; and this may be gradually attained and gradually lost. Here is matter for much interesting inquiry.

7. GALTON's regression is very important. Suppose we sow seeds of a self-fertilizing plant: and suppose that we know the amount by which it deviates from the

[1] DUNCKER, ROUX's *Archiv,* Vol. VIII, p. 163.

[2] GALTON, *Natural Inheritance,* and Proceedings Royal Society, Vols. 40 and 45; and ED. VERSCHAFFELT, *Correlatieve Variatie by planten.* Botan. Jaarboek, VIII, p. 92.

[3] Variability can also be influenced by grafting and inoculation. See L. DANIEL, *Compt. Rend.,* 1894, T. CXVIII, p. 992.

mean of its ancestors in respect of certain characters. Then we determine the curve describing the result of our sowing. As a general rule, the mean of any character in the filial generation departs less from the normal, than the character in question borne by the parent plant does. According to GALTON, the relation between these two deviations is a constant one: the mean deviation of the children amounts to about a third of that of their parents. The question whether this is a universal principle naturally suggests itself; the experiments which I have made hitherto seem to point to the conclusion that it probably is.

8. Does this regression remain the same even when selection is continued for several generations? In other words, does the mean of a race never amount to more than a third of the value attained by the seed bearers chosen in every generation? Does the race in spite of its improvement persist in this relation to its progenitors, that is to say, does it lag at every generation relatively further behind the selected individuals which produced it? It seems to do; at any rate the decision of this point dominates the theory of the origin of species by the natural selection of individual variations.

9. QUETELET'S law enables us to calculate from a curve of variation the number of individuals that will exhibit a desired degree of deviation from the mean. It seems that this chance even in the case of small differences is a very remote one demanding as it does millions of individuals. At any rate it is desirable to make such calculations for as many cases as possible.[1]

10. Artificial selection is a device for reaching a cer-

[1] See DUNCKER, Biolog. Centralbl., 1898, p. 571. For each additional 1000 individuals the range of variation only increases as from 1 to 1.049.

tain magnitude of deviation from the average, with a minimum expenditure of trouble. Is this its only significance? Does the number of individuals with the undesired qualities diminish exactly at such a rate as we can calculate beforehand? That is to say, is regression independent of the ancestry of a given parent; in other words, does it make any difference whether the seed parent is the result of repeated selection, or is picked from a single sowing on a much larger scale?

11. In such experiments attention should be paid to one character and one only; although interesting results may often be obtained by measuring a second or even a third character as a sort of collateral inquiry. The selections carried out by breeders involve as many characters as possible; on account of correlations the improvement of the chief features can be carried further in this way, than would otherwise be possible. Such experiments should be made with a purely scientific end in view.

12. In starting an experiment attention must always be paid to the individual vigor of the seed-parents. If this does not happen to coincide with the desired deviation, it is advisable to take both the strongest individuals and those exhibiting the greatest deviation, as seed-bearers and to compare the posterity of the two.

13. There is a particular kind of selection experiment which should be carried out a great deal more than it is. I mean one which would start by choosing as seed-parents plants with the smallest petals, the smallest fruits, those with the least degree of hoariness or the least number of spines, with the palest color in their petals, with the smallest number of stamens and carpels and so forth. According to the theory of natural selection such an ex-

periment should result in the origin of apetalous, fruitless, glabrous, spineless, white-flowered, unisexual or sterile plants and so forth. Whereas of course on the mutation theory this would not happen; provided that crossing was rigidly excluded from the experiment.

14. What we must aim at is a complete control of variation. We must become so thoroughly acquainted with the underlying factors that we can predict the results of our experiments.

V. THE ORIGIN OF SPECIES BY MUTATION.

§ 21. SPECIES, SUBSPECIES AND VARIETIES.

We saw in the second chapter that species cannot have originated by the natural selection of the extreme variants afforded by fluctuating variability.

We have therefore now to show that the observations which have been made on this subject can be simply and completely explained on the hypothesis of sudden changes. When such transformations occur among cultivated plants —and they often do—they are called spontaneous or, as DARWIN called them, *single variations*: moreover they are almost always inherited, if not in their entirety, at any rate to a very considerable extent.

We may express therefore the essence of the Mutation theory in the words: "*Species have arisen after the manner of so-called spontaneous variations.*" And in our critical survey of the facts we therefore have to consider how far the information at our disposal justifies this view.

In order to be qualified to discuss this question we must first of all make quite sure what we understand by the term "species" and, more important still, we must form a clear idea as to which forms we are going to regard as the units of the natural system. For it is only in the case of the *real* units of the system that we can

hope to obtain experimental proof of their common descent: the theory of Descent as applied to groups of these units is, and will probably always remain, a comparative science.

At the time when the Linnean view that species had been separately created was generally accepted, it was naturally a very important matter to decide which forms should be regarded as species. I have already endeavored to give some account of the broad features of the controversy which raged round this question during the period just before DARWIN's work appeared.[1]

Since the hypothesis of special creation of species was given up, the view that the Linnean species really were the units of the system was fostered by the persistence of binary nomenclature. But we are liable to forget that these species do not correspond to the units which exist in nature, but to groups of them. This is a fact which is clearly recognized and repeatedly asserted by the best systematists.[2] LINNAEUS himself, as we have seen, regarded his species as groups[3] and not as simple things, and DE CANDOLLE often speaks of them as collective.

The classification of plants into groups called species has exactly the same value and meaning as their classification under the headings of genera, families and so forth. So long as our knowledge as to what are the real units of the system is as incomplete as it is at present, systematists and students of distribution, no less than evolutionists will have to be content to deal with

[1] See chapter II, pp. 16-28.

[2] ALPH. DE CANDOLLE, *La Phytographie*; and *De l'Origine des Espèces cultivées*, 1883, p. 372.

[3] A good example of this is afforded by the species Homo sapiens.

the compound Linnean species and to regard the small local or elementary species as subsidiary to them.[1]

But it is clear that this conception of species must result in incomplete investigation and in fallacious conclusions. For example it is well known that the geographical distribution of species is analogous to that of genera; but it is evident that we should go far astray if we forgot that species like genera were collective entities. The distribution of elementary species, in the geographical region of the Linnean species which they compose, is very rarely made the subject of inquiry, yet it is just this point which is of the very greatest significance as bearing both on the origin and distribution of organisms. According to JORDAN every species, as well as every genus, has a geographical center where the distinct component elementary species are most abundantly represented, growing as they do close together on the same spot, whereas at the circumference of the region inhabited by the species its elements become few and far between.[2]

It is the actual theory of descent itself that would profit most by a proper appreciation of the conception of species. This theory which is recognized in morphology, embryology, in systematic work and in comparative anatomy as the guiding principle of all speculation and inquiry has remained almost without influence on experimental biology. At first it raised the hope that science would succeed not only in discovering the

[1] As is very properly done in the classification of parasitic fungi where some species are given a higher rank and embrace a certain number of species of a lower rank. See for example KLEBAHN in PRINGSHEIM's Jahrb. für wiss. Botanik, Vol. 34, p. 395.

[2] A. JORDAN, *De l'existence d'espèces végétales affines*, 1873, pp. 4-8.

common origin of all species but in bringing the origin of species within the range of direct observation and even in placing in our hands a certain amount of control over these natural processes.

But we are to-day just as far from this goal as we were in DARWIN'S time. The opponents of the theory of Descent have from the very beginning argued that we ought at least to be able to observe the origin of species and, perhaps, even to effect it experimentally. This criticism must even now be recognized as fully justified, although it is of course no longer one on the answer to which the validity of the doctrine of Descent depends.

It is just at this point that the prevalent confusion over species becomes most evident. What shall we make the object of observation and experiment? Our opponents answer: "The origin of the ordinary Linnean species of the systematist." But these are artificial groups whose limits can be altered by the personal taste of any systematist and are indeed as a matter of fact much too often so altered. The origin of such a species, like that of a genus, is a historical occurrence and it can neither be repeated experimentally, nor can the whole process be observed.

A plant-form can only attain the rank of a systematic species by producing a series of new forms and by the subsequent elimination of those which formerly related it to its parent form. It is obviously as impossible to observe the origin of an artificially circumscribed group like this as it would be to observe that of a genus or family.

The object of an experimental treatment of these phenomena must assuredly be to make the origin of the units which really exist in nature the subject of experi-

ment and observation. We must deal not with the origin of the groups made by the systematist but with those which are presented by nature.

There is no question that these elementary species often do arise in the garden and in agricultural practice. But in the first place they are only noticed when they have become established and when therefore the chance of observing the mode of their origin is irrevocably lost. And in the second place we smooth the matter over by calling the new forms "Varieties."

What are varieties? In wild plants they are usually very different from what they are in cultivated ones. Or rather the term variety has a number of definitions none of which is definite enough. In the eyes of those who perhaps unconsciously were anxious to maintain the supernatural value of species—and there are many of them even now—all forms, not the result of crossing, the history of whose origin is more or less accurately known, are called "varieties," Thus, all elementary species arising under cultivation fall into this category. Gardeners as a rule often draw no distinction between "varieties" and "kinds" on the one hand and between these and species and hybrids on the other.

The description of all forms with whose origin we are familiar, as varieties, opens the door to endless misuse of the term. On this ground alone therefore it ought to be given up. Even some of the best known authors of pre-Darwinian days thought that they could prove the common origin of a group of species by describing them as varieties of a species of a higher order. In this way NAUDIN for example, according to WALLACE, "proved" that the thirty species of melons, which had been recog-

nized up to that time, were only varieties.[1] And it will obviously continue to be impossible to demonstrate the origin of a "species" so long as this demonstration is regarded as "degrading" the form in question to the rank of a variety. This would become a mere juggling with words.

The conception of a variety held by those who are the best qualified to judge, rests on the view that a single character is not sufficient to confer specific rank on a given form. A beautiful example is afforded by the case which we have already mentioned of *Datura Stramonium* and *Datura Tatula.* Each was regarded as a species by LINNAEUS himself, but they have been united to form a single species by more recent authors on the ground that *Tatula* is only distinguished from *Stramonium* by the possession of a blue pigment in its flowers, stem and petioles.[2]

This limitation of the idea of a variety is manifestly desirable scientifically, especially for the reason that the distinguishing feature is very often due to the loss or latency of a character: absence of Petals, of Hairs, of Thorns, of Color in the flower and so forth. Such cases afford the best examples of what we ought to call a variety. But it should not be forgotten that the evidence for the relationship of such forms to their species ordinarily rests only on analogy; and not, or very rarely, on actual proof.

Such varieties are just as distinct and just as constant in cultivation as the best species. If it is still considered proper that they should be called varieties, then it fol-

[1] WALLACE, *Darwinism,* p. 87

[2] In my opinion, *Stramonium* is regarded quite wrongly as the species and *Tatula* as the variety. Every analogy points to the blue as the older and the white as the younger form (See Fig. 5 on p. 31).

lows that varieties are nothing less than a particular form of species. *Varieties are only small species,* as DARWIN has said.[1]

JORDAN's elementary species are distinguished from one another not by one peculiarity but in nearly all their characters. This is an extremely important point. There is absolutely no justification for regarding them as varieties. If we wish to treat them as subdivisions of the old species they must be called subspecies. I prefer to call them elementary species. DARWIN speaks repeatedly of *specific elements* when he is referring to their individual characters.[2]

There is little prospect that an agreement between all the workers in this field will ever be brought about. *Theoretically* in my opinion we should be perfectly justified in applying the coveted distinction of "species" to these elementary forms, whose limits are not set by our imagination. But *practically* it is for many reasons more convenient to refer to the artificial groups of these, that is, the collective species, simply as species. Where we are concerned with the investigation of the origin of a single species we mean of course an elementary one. The other species are groups whose origin is a matter of history and cannot for this reason be dealt with experimentally.

Thus we see that Linnean species are collective and artificial whilst JORDAN's species are single and real. Each collective species consists of a larger or smaller group of subspecies or elementary species; in the deter-

[1] *Life and Letters,* II. p. 105. DARWIN's more famous aphorism that *varieties are incipient species* is less happy. We know nothing about the age of most varieties.

[2] E. g., *Variations in Animals and Plants,* II, p. 23. Each of these elements is represented in the germ, according to the theory of Pangenesis, by a unit, the *Pangene.*

mination of the limits of these groups the systematist is guided almost entirely by the gaps which have arisen by the disappearance of more or less numerous subspecies.

With regard to the nomenclature, it would perhaps be better if the binary system were replaced by a ternary; to retain the Linnean specific names as much as possible and to write after them the name of the elementary form.[1] The idea of a variety should be strictly confined to cultivated forms.[2]

§ 22. SPECIES IN NATURE.

The species of the systematist are compound species; they consist of a greater or smaller number of subspecies which breed true when tested. The larger the geographical area inhabited by a species, the larger is the number of component subspecies: they are concentrated in the center of the area and become scattered towards its periphery.

In local floras therefore as a rule each species consists of only one or very few elementary species.[3] The species of such local floras do not exactly agree in neighboring districts.[4] From France alone JORDAN brought

[1] This course is adopted by WAAGEN in BENECKE, *Geognostisch-paläontologische Beiträge*, 1876, Vol. 2, p. 187.—An example: any one can guess the meaning of *Draba verna leptophylla* whilst *Erophila leptophylla* has no meaning except to the initiated.

[2] Subspecies are not to be regarded as subsidiary to, nor as derived from the species; for each species consists of a group of subspecies. The only thing that can be said in favor of the conventional assumption of a *forma genuina* is that it is convenient.

[3] Only one elementary species of *Draba verna* so far as I can find occurs round Amsterdam and the towns in its neighborhood: it agrees with JORDAN'S *D. leptophylla*.

[4] For example *Senecio Jacobaea* is common in the neighborhood of Haarlem, but always without ray-florets, whereas in the adjoining dunes near Leiden it is only found with these florets.

together over 50 species of *Draba verna*[1] in his garden,[2] and from other countries in Europe, especially from England, Italy and Austria, about 150 more, so that in 1873 he had more than 200 forms in cultivation.[3]

This richness in forms, or polymorphism as it is called, of the so-called "good" species is quite a general phenomenon.[4] DARWIN repeatedly called attention to it and argued that as a result of it the most widely distributed types had the best chance of giving rise to new species and so of gradually becoming genera.[5] In the case of rare forms he showed the prospect of doing so to be much smaller.

Very few plants are as rich in subspecies as *Draba verna.* Perhaps *Viola tricolor* comes next[6] with its well-known subspecies *Viola arvensis* which is itself a collective form.[7] In Germany or France the average number of subspecies per species may be placed at 2 or 3, for the whole of Europe the average is perhaps about 10. If all these forms were noted and described the Flora of Europe would be increased tenfold, which would be most inconvenient. But just as there are valuable treatises which only deal with the genera or at any rate only with these and their more important species, so it would be the business of the ordinary Floras to describe the species and their more important subspecies. The task of deal-

[1] See Fig. 3 on page 22.

[2] *De l'origine des arbres fruitiers,* 1853.

[3] *Des espèces végétales, affines,* p. 13, 1873.

[4] It is often spoken of as "Variability": but this cannot conceal the fact that the elementary species which compose the species are constant, and independent of one another.

[5] WALLACE, *Darwinism,* p. 80 and 98.

[6] A. JORDAN, *Observations sur plusieurs plantes nouvelles,* 1846-1849, Vol. II, p. 7.

[7] See Fig. 4 on page 23.

ing with all the elementary forms that exist must be the duty of monographs of a greater degree of completeness.[1]

When it is a question of the origin of one elementary species from another this material is absolutely essential to the student of evolution. When however our object is the study of the relationship of the larger groups it certainly constitutes a mere dead weight, the fact of whose existence one is only too often tempted to suppress. But I can see no reason why these two branches of inquiry should not exist side by side. Nothing but a belief in the supernatural value of the Linnean species can stand in the way.

Fig. 33. *Potentilla Tormentilla,* with narrow, broad and intermediate petals representing three constant subspecies found in nature.

In the natural state it is only very rarely that elementary species are distinguished by a single or by two or three characters[2] (Fig. 33); they usually differ in all their organs and characters. A complete diagnosis often requires a whole page. The *tout ensemble* of the plant is quite distinctive; and the practised eye can recognize the various forms at a distance.[3] This is especially so in the case of cul-

[1] Compare, for example, the *Flora Europae* of M. GANDOGER, which gives the elementary forms for all the more important species, but only refers to their characters in short dichotomous tables (27 vol.).

[2] On the heaths near Amsterdam there are to be found three forms of *Potentilla Tormentilla,* one with narrow, one with broad and one with intermediate petals; I saved seeds from each of these forms and found them to be constant.

[3] Or they may be quite or nearly indistinguishable externally and differ from one another only in fundamental physiological characters as for example in the choice of hosts in the case of the Rusts—facts

tures where groups of many individuals of the different types grow close together. The characters are sometimes of such a kind that they are easily recognizable even on dried material; but they very often disappear entirely or partly when the plants are pressed.

The constancy and thus the distinctness of the local species can only be proved by cultivating the plants from seed.[1] Experiments of this kind have been carried out on a large scale by KOCH and FRIES and other well-known systematists but especially by JORDAN and his pupils. In many cases these experiments have been repeated and always with the same result. THURET and BONNET grew 14 of JORDAN's species of *Draba verna*, 4-6 species of *Papaver dubium*, for about 7 years and convinced themselves of the constancy of these forms.[2]

This statement is supported by the high authority of DE BARY, who satisfied himself as to the constancy and systematic distinctness of the numerous subspecies of *Draba verna*,[3] as the result of his well-known researches, which were continued and published after his death by F. ROSEN. This splendid work has received full recognition, but it has not had the effect which DE BARY evidently hoped it would have on his contemporaries, of directing research more generally into these channels.

A similar state of affairs obtains in zoology. Every zoologist knows, as BATESON remarks,[4] that in the case

which we owe to the exhaustive and important researches of ERICKSSON.

[1] Conclusions based on comparative study only should never be regarded as proofs in this field. See the *Flora Europae* of GANDOGER.

[2] J. COSTANTIN, *Accomodation des plantes*, Bull. scientif. publié par GIARD, Vol. XXXI, p. 507.

[3] F. ROSEN, *Systematische und biologische Beobachtungen über Erophila verna*, Bot. Zeitung, 1889, No. 35.

[4] W. BATESON, *On Progress in the Study of Variation*, Science Progress, Vols. I and II, 1897-98. Vol. II, p. 1.

of many species the individuals differ according to the region which they inhabit, and that by means of these differences the species can be split up into local races. The differences may be very slight and often only visible to the initiated, and yet perfectly constant. But these facts are far from being appreciated as much as they deserve.[1]

§ 23. SPECIES IN CULTIVATION.

Just as wild species at present consist of a larger or smaller number of constant and independent subspecies, so presumably will it have been with those species which man has brought into cultivation.

PLINY was acquainted with the different kinds of a number of fruit trees, for example 43 sorts of pears, 29 of apples, 10 of plums, 8 of cherries and so forth. The Romans knew at least two sorts of beet, several kinds of which grow wild in the Mediterranean region.

In about the year 1600 OLIVIER DE SERRES described in his *Théâtre d'agriculture* the cultivated plants that were known at that time. He refers also to the main types of our modern vegetables. He mentions 61 varieties of pears, and 51 of apples, and also the commonly grown sorts of beet. Whence all these forms arose we do not know. It is possible that they arose *in* cultivation; it is even possible that they arose *as the result* of cultivation. But it is equally possible that they existed *before* it, growing wild either together or in different places, and that all or most of them were taken over into cultivation as such. For there is absolutely no ground for the belief that the plants known to agriculture were *only*

[1] See also DUNCKER, ROUX'S *Archiv*, Vol. VIII, 1899, p. 164.

once found by man in nature and only once brought into cultivation.

So long as the chief concern of biologists was to establish the theory of descent there was some use in elaborating the probabilities in this sphere. But now, it seems to me that it will suffice if we recognize the lack of historical information on this point.

A favorite theme for discussion is the question whether wheat owes its origin to a few or to many wild forms. For whether we are to assume that wheat has "varied" in a large or small degree during its cultivation depends on the answer to this question. It seems far more likely that wheat, just like *Draba verna,* was originally composed of a vast assemblage of subspecies in the wild state.[1] And as fertilization in wheat takes place mainly before the flowers are open, it is evident that many kinds can maintain themselves side by side in the same field, provided of course that they are really constant.

The history of this subject contains a chapter which has a very strong bearing on this point. It concerns Colonel Le Couteur's cultivations in Jersey at the beginning of the nineteenth century.[2] He was visited by Professor La Gasca who pointed out to him that his field of wheat, far from being a uniform culture, consisted of at least 23 distinct sorts growing together. The natural supposition was that some of these sorts would have a larger share in the harvest than others. Le Couteur therefore harvested the seeds of typical individuals of these sorts separately and carried out comparative

[1] Of all cultivated plants the cereals have changed least according to De Candolle in *l'Origine des espèces cultivées.*

[2] Von Rümker, *Getreidezüchtung,* p. 67.

sowings of pure bred kinds for a space of a few years to find out which of them were the most valuable. The offspring of these sorts proved to be pure and constant; and his original field must therefore have contained simply a mixture of these sorts. Le Couteur continued to grow the best of the kinds thus purified with such success that he put them on the market with no small advantage to himself; even now some of them are still very well known, as for example the *Bellevue de Talavera.*

Wheat was therefore at that time a mixture of different sorts; Le Couteur seems to have been the very first to isolate these units.[1] And even now the common types of wheat are still mixtures. The mixture maintains itself without artificial selection, but the pure form does not.[2]

Later, Patrick Shirreff in Scotland worked on the same lines as Le Couteur with various forms of cereals. He used to look in his own fields and in those of his friends for striking and apparently better examples: then he sowed their seeds separately and examined their offspring. As a rule they turned out to be constant and often very productive. In this way he found the original of *Mungo swells wheat* in 1819, *Hopetown oats* in 1824, *Hopetown wheat* in 1832, and later *Shirreff's oats.*[3] They were absolutely constant and as soon as a sufficient quantity of seed had been obtained by cultivation for two

[1] At that time nobody thought of improvement: the idea did not arise till about 50 years later.

[2] See p. 98.

[3] V. Rümker, *loc. cit.*, p. 70. See also the account of Dr. Hesse's travels in Landw. Jahrb., VI, 1877, p. 850 et seq., and Shirreff's *Improvement of Cereals,* London, 1873.

or three generations they were put on the market without further selection.

Space does not permit us to treat further of Le Couteur's and Patrick Shirreff's work. Suffice it to say that they show us in a general way that wheat, barley and oats[1] were at that time mixtures of perfectly constant subspecies exactly as we have seen that the species of wild plants are. But we know as little about their origin in the one case as we do in the other.

One of the most frequently discussed questions in practical horticulture is that of the origin of fruit trees, especially of the modern improved kinds of apples and pears. There is no doubt about the common origin of these forms. The question is only whether their common origin merely follows from the theory of descent or whether it is historically traceable. The latter is certainly not the case with most of the chief types; the past history is only known with certainty in the case of some of the recent sorts.

It is to the Belgian breeder Van Mons that we owe the most valuable information on this subject that we possess. In the first half of the nineteenth century he put many of our well-known kinds on the market.[2]

[1] Rye, which may be wind-fertilized, behaves differently.

[2] The literature on this subject seems to be little known and is difficult to get hold of: I have not succeeded in seeing the works of Poiteau and Chandèze. The following is a list of the most important:

Van Mons, *Arbres fruitiers ou Pomonomie belge*, 2 vols, 1835. Quotations from it will be found in Jordan's *Arbres fruitiers*, pp. 38 and 94..

Poiteau, *Théorie de Van Mons ou notice historique sur les moyens qu'emploie Van Mons pour obtenir d'excellents fruits de semis.* Ann. Soc. d'Agric., Paris, 1834, Vol. 15.

G. Chandèze, *La Théorie de Van Mons concernant la production de nouvelles variétés fruitières.* Belgique horticole, 1877, p. 354. Bot. Jahrb., V, p. 761.

Godron, *De l'Espèce*, II, p. 101.

Van Mons expressly stated that he himself had not originated any new forms: "La nature seule crée."[1] He found all the sorts which he cultivated and put on the market, growing as such in the wild state[2] and, as it happened, almost all of them in the Ardennes. The wild plants were thorny and their fruits small, tough and woody. As the result of being sown in a garden and under the influence of another climate[3] they regularly lose their thorns and the tough consistency of their fruits, which become larger, fleshier and juicier. But the differences in form, color and taste and other valuable characters arose neither in, nor as a result of, cultivation; they already existed in the wild forms. His new kinds are nothing more nor less than already well-known cultivated forms[4] which he has improved in respect of size and juiciness, by selection for two or three generations[5] without altering their varietal characters in the very least.[6] Van Mons was fully aware of the independence and constancy of these forms and it should be noted that he speaks of them as subspecies and not as varieties.

The best way to raise a new type for the market is not to sow the seeds of the best sorts already in cultivation but those of a fruit which, be it ever so puny, belongs to a hitherto unknown type.

It seems that most of the new sorts that have been raised by other breeders have arisen in the same way. For example the splendid *St. Germain* pear owes its origin to a single tree found by chance in the *Forêt de St. Germain* near Paris; *Bézy de Chaumontel, Bergamotte Sylvanche*, and *Virgouleuse* are also due to a lucky find.

[1] *Pomonomie,* I, p. 445,
[2] *Loc. cit.,* p. 406, 444.
[3] *Loc. cit.,* p. 410.
[4] *Loc. cit.,* II, p. 208.
[5] *Loc. cit.,* p. 462 and II, p. 208.
[6] *Loc. cit.,* I, p. 415.

Bailey[1] has recently given a very striking example which illustrates this point. Mr. Peter M. Gideon sowed a vast number of apple seeds and from these he got a single plant whose fruit he ultimately put on the market as the *Wealthy Apple,* because he made his fortune by it. This apple is now one of the most favorite and widely known in Minnesota.

Mr. Gideon tells the story of how he got this magnificent fruit as follows. For nine years he sowed apple seeds so as to raise about a thousand young trees every year. But all this led to no result. Then he happened to buy a small basket of apples of a foreign kind in Maine: they provided him with about 50 seeds from one of which his *Wealthy Apple* arose. Sowing on a large scale had no result; sowing on a small scale but from a new form fulfilled his highest expectations.

Our argument is supported by the following evidence. If apples and pears are allowed to grow wild they are well known to revert to the type of the crab-apple and the wild pear in a few generations. But each sort retains the features characteristic of it; they do not all revert to one and the same wild form.

Whence does the host of wild sorts of apples and pears arise? We do not know. There are some who assert that they have arisen in cultivation and have then run wild. But this would hardly account for the large number of new sorts that have been obtained.

It is the same with most cultivated plants as it is with cereals and fruit trees: almost every species consists of more or less numerous subspecies about whose origin we know nothing at all.

Flax, the red clover and the poppy are very good

[1] L. H. Bailey, *Plant-breeding,* New York, 1896, p. 108.

examples of plants with such subspecies. The chief types of *Chrysanthemum indicum* were imported as such from Japan into Europe; the newer sorts have almost all been obtained by crossing them. A great variety of other examples can be easily collected.

Fig. 34. *Sedum crispum* after MUNTING, 1671.[1]

Many so-called varieties and even many monstrosities have been known since the time when the species to

[1] ABRAHAM MUNTING, *Waare Oeffeninge der Planten*, 1671, p. 357. MUNTING's *Sedum crispum* evidently is the same as *Sedum cristatum* SCHRAD. (*Sedum reflexum cristatum*); the monstrosity must therefore be more than two centuries old. Since MUNTING's time fasciation in this species has repeatedly been observed and recorded. Cf. PENZIG, *Teratologie*, I, p. 467. The character is strongly inherited. I raised from seed a square-meter bed full of plants with more or less flattened branches, some of which I have photographed and reproduced in Fig. 35. Normal cylindrical or atavistic branches are shown both in the above figure from MUNTING and in that from my own culture (Fig. 35 at.).

which they belong were introduced; and have been described and drawn in early works on the subject. ABRAHAM MUNTING gave a long list of them in the year 1671.[1] In it will be found examples of double flowers of *Vinca, Colchicum, Hepatica, Cardamine, Cheiranthus Cheiri, Papaver, Viola, Caltha, Althaea,* and others; of white-flowered forms of *Ononis, Syringa, Centaurea, Digitalis, Fritillaria, Hepatica* besides white strawberries, white

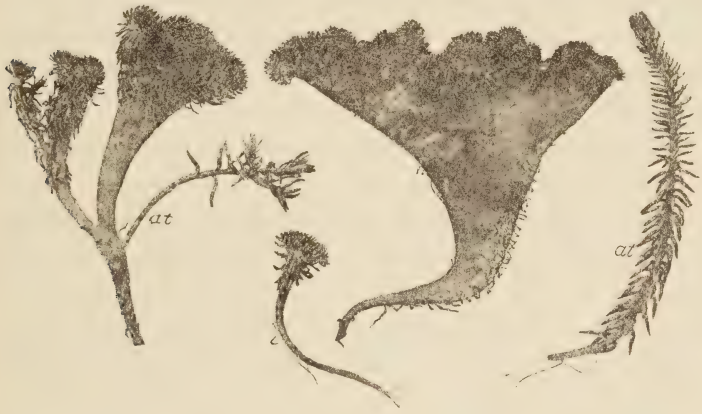


Fig. 35. *Sedum reflexum cristatum.* From nature, 1900, with expanded and ordinary (*at*) branches.

raspberries and red gooseberries, and double *Bellis* and *Matricaria.* Also proliferating forms of *Bellis, Calendula, Helianthus* and *Scabiosa,* fasciated Crown Imperials, *Plantago major rosea, Primula veris,* and *P. Auricula* with a double Corolla, fasciated *Sedum* (Figs. 34 and 35), *Celosia cristata, Amaranthus cristatus,* etc.

Moreover hundreds of varieties of the more important garden plants, e. g., Hyacinths, Tulips and Ranunculus were known at that time.

[1] *Waare Oeffeninge der Planten,* Groningen, 1671.

Many forms which are put on the market as new are, from our point of view, really quite old. I mention as an example the famous double Lilacs which Victor Lemoine of Nancy put on the market in the '80's. They consist of a number of new and in many respects excellent varieties which have now found a place in many gardens and parks. They were offered as new; and I was anxious to find out how the "doubling" had been attained. I went, therefore, in 1892 to Nancy and asked M. Lemoine. After he had shown me his plantations of Lilac he told me the following story of their origin. "In 1870 I happened to see in a garden in Luxembourg, a double specimen of *Syringa vulgaris azurea plena,* a little-known form which is seldom seen in gardens. When some years later I came to think of growing Lilacs I simply bought this plant and crossed it with almost every variety on the market." This was the way in which he got his novelties. But as to the origin of doubling he was completely in the dark. Later I found that Munting had mentioned the double form as early as 1671.

We know just as little about the origin of the Cactus-dahlias which threaten to supersede all other kinds owing to their great variety, and to the splendor of their flowers. They are the result of a cross between one single plant and numerous older varieties. When I visited Mr. Van den Berg in Jutphaas who introduced this novelty, he gave the following account: "Many years back (1872) I asked a correspondent of mine in Mexico to send me a case of bulbs, roots or rhizomes of any kind of foreign plants he could possibly get hold of. The contents of the box reached Holland in very bad condition: almost everything was rotten; in fact everything but a single tuber which however produced a shoot. This plant was

the first *Cactus*-Dahlia. All efforts to find the same form, in the district where my correspondent lived, were in vain."[1] The plant was there; but how it arose we do not know.

It is just the same in many other cases, and with the most important types too. The breeder is delighted when he sees a new form; but as to *how* it arises he is generally ignorant. It often happens that they arise singly in sowings on an enormous scale; in which there is a greater likelihood that the seeds will be of different stocks, than in small ones. In this way D. B. WIER got his cutleaved maple in a sowing of about a million seedlings.[2] And in the same way DONKELAAR got the first double Dahlias in a culture of about 10,000 plants, and so forth.

There is no object in citing more instances especially as most of the early ones are to be found in DARWIN's works.

We may conclude therefore that even among cultivated plants, species are mixtures; consisting, as they do, of independent often numerous sorts of subspecies which have been found as such in the wild state. This fact is well known to many breeders and botanists: though the earlier botanists were more familiar with it than modern ones are. Hence the often repeated saying,[3] "If you want to raise a novelty you must first possess it!"

§ 24. SPECIES AND SPECIFIC CHARACTERS.

The reader is now in a position to understand what I mean when I say that our business is not really with

[1] See VAN DEN BERG, *in* Gardeners' Chronicle, Nov. 8, 1879; and W. MILLER, *The Dahlia,* in Bull. Ithaca, No. 128, p. 127.

[2] L. H. BAILEY, *Plant-breeding,* 1896, p. 109.

[3] JORDAN, *Arbres, fruitiers,* p. 96.

the origin of species but with the development of specific characters.

The diversity of organic forms is due to the existence of a vast number of differentiating characters. And the question we have to answer is "how have these characters arisen?"

Subspecies become species by extinction of intermediate forms. New species can arise by crossing when the peculiarities of two forms already existing are united to form a single new one; and so on. But these are not cases of the origin of specific characters. Many species and even genera and still larger systematic groups have arisen by these characters disappearing or becoming latent. The origin of the monocotyledons from the dicotyledons is regarded by some as coming under this head (DELPINO). But loss and latency are obviously special cases which do not directly touch the main question of progress in the animal and vegetable kingdom.

The question is not how many characters peculiar to itself must an animal or plant possess to justify its elevation to specific rank, but: how have these characters arisen, or how can they arise?[1]

In other words: the mutation and the actual process of mutating must become the object of investigation. And if we once discover the nature of this process, not only will our insight into the actual relationship of living organisms become much deeper, but we may even hope that we may be able to gain some measure of control over the formation of species. If the breeder has obtained control over variability why should he not obtain it over mutation as well?

[1] "These factors are the units with which the science of heredity has to deal." *Intracell. Pangenesis,* p. 9. For their association in groups see pp. 21-22 and 33.

It is clear that we can only advance by very small steps dealing at each step with a single mutation. But even single mutations may be of enormous importance in horticulture or agriculture. Much that now seems unattainable may come within our power if only we can obtain some insight into the fundamental principles involved in mutation. There lies here a wide field of work the results of which will be as important to the biologist as to the practical man.

§ 25. MUTATIONS IN CULTIVATION.

In a preceding section (§ 23) I endeavored to show that many of the elementary species which exist in a state of cultivation had arisen before they were introduced into it. But it does not follow that this is always the case as JORDAN, KERNER and others believe.

On the contrary in many cases there is historical evidence which at least makes it highly probable that mutations occur in the garden and the field no less than in the wild state. But it usually happens that the new form is not seen until it is already established; how, when and where it arose cannot be discovered, or at most only with a small degree of certainty.

According to the theory of selection the origin of a new form is a gradual process which we can observe whilst it is taking place. But the evidence at our disposal does not support this theory. It is true that forms which have arisen suddenly exhibit a high degree of fluctuating variability and so give the selector the opportunity of intensifying the new character. But that is a very different matter from the gradual origin of the new character.

Good examples of mutations can be found in agricultural and horticultural literature. But before I give a selection of them I must point out how clearly the distinction between races and subspecies is appreciated by practical authors. Prof. KURT VON RÜMKER in his often quoted *Introduction to the Breeding of Cereals* divides his treatment of methodical selection into two parts. One of them deals with selection with a view to improvement, the other with selection with a view to the origin of new forms.[1] The object of the former, he says, is to fix characters already present, to stamp them so to speak, and to intensify desirable qualities.

New forms, however, arise when the changes "do not consist merely in continuous improvement along one line but in the production of new qualities as lateral offshoots." Such changes occur now and then in our fields and are known as spontaneous variations. "Nothing is yet known with certainty about the origin of such spontaneous variation and still less about the causes of their origin." All that we know is that they are inherited.

After these quotations from VON RÜMKER the common phrase "the production of new forms" will sound, to say the least, exaggerated: we should be nearer the mark if we spoke of the search for new forms (and of their subsequent improvement, in the usual sense of the term).

The awnless form of BESELER's Anderbecker Oats is a very famous example of a form which was found ready to hand in the fields.

I propose to give now a series of further examples. In almost all the cases the new sorts have come absolutely true to seed from the very beginning when the possibility

[1] P. XIV, and 56 and 83.

of crossing has been rigidly excluded. Sometimes the new character appears very slightly developed in the first instance as in the case of "double" flowers. In such cases the characters have to be improved by selection. In some the variation appears once and for all, in others it continually reappears. It is well known that every breeder should look anxiously for possible novelties; but when he has found one, it depends on him and on him alone whether it attains its full beauty.

The origin of the new form is emphatically due to chance and not to the skill of the breeder, as it is in the improvement of races.

Chelidonium laciniatum Miller, a subspecies of *Chelidonium majus,* is one of the most beautiful examples because more is known about its origin than about that of almost any other plant, thanks to the painstaking inquiries of E. Roze.[1] He gives the following history of it.

About the year 1590, Sprenger, an apothecary in Heidelberg, found in the garden where he grew plants for his business (amongst which was *Chel. majus*), a new form of *Chelidonium* which differed from *C. majus* in the possession of deeply cut leaves and petals. He called it *Chelidonia major foliis et floribus incisis* and sent some examples to Jean Bauhin, Gaspard Bauhin, Clusius, Plater and other well-known botanists of his time. All of them declared that the plant was unknown to them and new. It had never been found wild before, nor has it been found since; although from time to time it has escaped from gardens. It comes absolutely true from seed, has maintained itself till the present day and is very generally grown in Botanical gardens. Miller,

[1] E. Roze, *Le "Chelidonium laciniatum" Miller,* Journal de Botanique, 1895, Nos. 16-18.

Roze and many others have tested its constancy by cultures extending over many years and have observed no reversion to *C. majus*. I have repeated the experiments with the same result.

We may conclude therefore that *C. laciniatum* arose about the year 1590. Unfortunately Sprenger does not say whence the seeds came which gave rise to it; whether

Fig. 36. *Chelidonium laciniatum*. A flower of it to the left. Below a flower of *C. majus*.

from seed saved by himself from *C. majus* or from some other source. The former is the more probable since otherwise he would have known from whence he had obtained it.

Transitions between the two species in question do not occur to-day any more than they did in Sprenger's

time. We may presume therefore that the younger form arose suddenly from the older one.

W. T. Thiselton Dyer has described a series of spontaneous variations of *Cyclamen latifolium,* a very interesting species from the fact that it is one of the very few garden plants with which crossing had not yet succeeded.[1] The supposition of a hybrid origin of its subspecies is therefore excluded. A form with horizontally projecting petals and another with hairy structures in its flowers, reminding one of similar structures in the flower of the Iris, have been described. The first form has arisen many times; it was at first thrown away as unsuitable for cultivation, but has since been put on the market. The incised petals also have arisen several times, for example in 1827, when they were described in the Botanical Register, but were subsequently lost. Since 1850 they have appeared in several nursery gardens. The hairy structures suddenly appeared in 1890 in the nursery of Messrs. Hugh Low & Co., although in a very rudimentary form. They were greatly improved by repeated selection, and after a few years put on the

Fig. 38. *Chelidonium majus.*

[1] W. T. Thiselton Dyer, *The Cultured Evolution of Cyclamen Latifolium.* Proceed. Roy. Soc., Vol. LXI, No. 371, p. 135.

market. They also appeared in France as early as 1885; but there they were not cultivated further. They exist both in the red and in the white variety.

Strawberries without runners belong to the species *Fragaria alpina* and are known under the name of GAILLON-*strawberries.*[1] Forms are known both with red and with white fruits.[2] The history of their origin is recorded by P. P. A. DE VILMORIN in the *Bon Jardinier.*[3] He found a single individual bearing this character in a crop of the ordinary *Fragaria alpina.* The seeds of this individual gave rise solely to plants without runners: the new sort was absolutely constant from the beginning.

The cauliflower and Kohl-Rabi were raised from isolated monstrosities of *Brassica oleracea.*[4] The *Chou de Milan des Vertus* likewise arose spontaneously from another sort of cabbage and soon became one of the most popular vegetables in the Paris market.[5] *Mercurialis annua laciniata* was discovered in 1719 by MARCHANT as a new form; since that time it has come true from seed.[6] That is the last of these examples I shall refer to.

Some species have appeared twice, or even more often, in localities widely distant from one another and under circumstances which almost completely exclude the possibility of a common origin. I may quote the example of the copper beech, to which Prof. J. JÄGGI has devoted an exhaustive historical monograph.[7] Three localities

[1] See Fig. 7 on page 34.

[2] VILMORIN ANDRIEUX et Cie., *Les plantes potagères,* p. 222.

[3] L. DE VILMORIN, *L'amélioration des plantes par le semis,* 2d ed., p. 48.

[4] A. P. DE CANDOLLE, Transact. hortic. Soc., 5, p. 1, quoted in Hofmeister, *Allgemeine Morphologie,* p. 565.

[5] VILMORIN, *L'amélioration, loc. cit.,* p. 19.

[6] GODRON, *De l'Espèce,* I, p. 160.

[7] J. JÄGGI, *Die Blutbuche zu Buch am Irchel,* Zürich, 1893.

for it are known. The Stammberg near Buch am Irchel in the Zürich Canton; a wood near Sondershausen in Thuringia;[1] a wood above Castellano near Roveredo in the southern Tyrol. The first locality was known as early as the 17th century; the second in the second half of the 18th century; the third only at the beginning of the 19th. In the same way *Fragaria monophylla* (Fig. 38) was found by FRIES in the neighborhood of Skarugata in Lapland; then it arose in a garden near Versailles about 1761 and is now to be found in many botanical

Fig. 38. *Fragaria vesca monophylla.* *a*, two leaves; *b*, a young plant on a runner with single, double and triple leaves—a case of atavism.

gardens.[2] *Fagus sylvatica aspleniifolia* was found in a wood in Lippe-Detmold and in the neighborhood of Paris.[3] *Alnus glutinosa laciniata* (Fig. 39) and *Betula alba laciniata* are found wild in Sweden and Lapland.[4]

[1] Mr. C. DÖRING in *Sondershausen* informed me, that this tree is still living; its foliage as well as that of its offspring is, however, only of a pale red. (Note of 1908).

[2] BRAUN, Abh. k. Acad., Berlin, 1859, p. 113; HOFMEISTER, *Allg. Morphologie*, p. 557 and 571; Bot. Zeitung, 1878, p. 283; ALPH. DE CANDOLLE, *Géographie botanique*, II, p. 1081.

[3] E. FAIVRE, *L'espèce*, p. 44; the former statement is from BRAUN, *Verjüngung*.

[4] BRAUN, *loc. cit.*, p. 332.

In the nursery gardens the same novelty often appears simultaneously in different places; as for example *Ageratum mexicanum nanum luteum* which arose about 1892 in both Paris and Erfurt.[1]

There is a series of varieties on the market, of the most diverse botanical species, of which it can be said that it would be practically impossible for them to grow wild. They have often been brought forward as evidence

Fig. 39. a, *Alnus glutinosa laciniata* with fruits; b, leaf of *Alnus glutinosa.*

Fig. 40. *Ranunculus acris petalomana,* a form which has become completely sterile by profuse petal formation. From a plant found in a meadow.

for the view that varieties arise suddenly *in cultivation* by so-called spontaneous variation or mutation. I recall those fruits which cannot dehisce as *Papaver somniferum inapertum* and *Linum usitatissimum* (*L. crepitans* is the only subspecies which open its fruits so as to scatter the seeds). Then there are the large and heavy seeds of cereals and some *Leguminosae* but especially of maize

[1] I was told this by Mr. Otto Putz, a nurseryman in Erfurt.

whose seeds seem to have no means of becoming distributed. Lastly there are the sterile varieties; Currants (Corinthian grapes), Bananas, many sorts of apples and pears, astrakhan grapes, some strawberries, the green rose, the green *Pelargonium zonale* and green Dahlias (of which I have cultivated two different sorts, one with elongated and the other with ordinary flat flower-heads). *Ranunculus acris* and *Caltha palustris* which have become sterile by petalomany (Fig. 40) and many other examples of this kind of doubling;[1] then there is the sterile Maize (Fig. 41) many examples of which have appeared in my own cultures but which, so far as I know, does not seem to have been noticed elsewhere.[2]

The great majority of forms which have arisen suddenly, be they varieties or subspecies, come absolutely true from seed; that is to say every single seed gathered reproduces the new form when sown, provided that the seed parent was fertilized with its own pollen, or with pollen from another example of the same form. Constancy is one of the properties of elementary species.

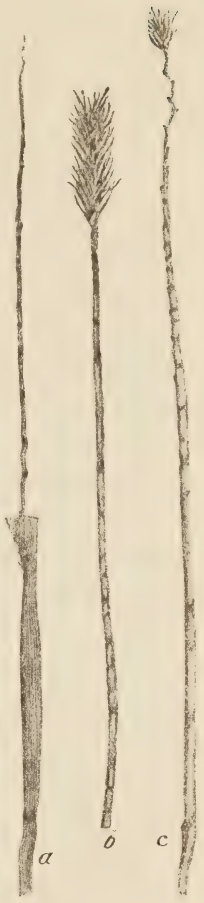


Fig. 41. *Zea Mays sterilis.* Three unbranched "panicles." a, without bracts; b and c, with slight bract formation at the tip.

[1] K. Goebel. Pringsheim's *Jahrbücher für wissensch. Bot.*, Vol. XVII, p. 207.

[2] *Over steriele Maisplanten,* Botan. Jaarboek Dodonaea, Vol. I, 1889, Table V, p. 141. *Steriele Mais als erfelyk ras, ibid.,* Vol. II, 1890, p. 109.

Apparent exceptions to this rule are so numerous that we might be inclined to doubt its universal validity. But in most cases it will be found that those who record such exceptions have paid no regard to the possibility of cross-fertilization by insects or by the wind. Crossing is certainly the simplest and most obvious explanation of them. The whole subject of so-called atavism in plants demands a careful re-investigation, for most of what passes as atavism in the nursery and private gardens is nothing more nor less than the result of accidental crossing. At least so my researches into these phenomena lead me to believe.

I shall however return to this subject and deal with it more thoroughly in a later section; and shall confine myself now to citing some of the more important instances of constancy.

The complete constancy of many varieties is well known. As for example in the case of *Matricaria Chamomilla discoidea* and the corresponding varieties of *Bidens tripartita* and *Senecio Jacobaea*. Also of *Datura tatula inermis*,[1] of *Ranunculus arvensis inermis*,[1] of the peloric varieties of *Antirrhinum majus*,[2] of *Nigella sativa apetala*,[3] of *Ilex Aquifolium* with yellow berries,[4] of weeping oaks and weeping birches,[4] of red-leaved *Berberis*,[4] of the peloric form of *Corydalis solida*,[5] of *Hordeum trifurcatum, Rubus fruticosus laciniatus* besides countless garden plants and vegetables (sugar peas, thornless spinach and so forth).

[1] Botan. Zeitung, 1873, p. 687.

[2] Masters, *Vegetable Teratology*, p. 227.

[3] Hoffmann, Botan. Zeitung, 1881, p. 410; a number of other examples are recorded here.

[4] Darwin, *Variation in Animals and Plants*, II, pp. 24, 26.

[5] Godron, *Mém. Acad. Stanislas*, 1868, p. 3.

I have already said that the so-called cases of atavism, brought forward as evidence against this constancy, are really cases of crossing. The copper beech illustrates this well. Its distinguishing character is reported as being inherited to a highly variable extent, according to the locality in which it lives. Sometimes all the seeds come true; sometimes only 20%. But as the trees in question grow amongst ordinary beeches, and as artificial fertilization is of course out of the question, they must usually be fertilized by pollen from the surrounding trees. If we want to draw any conclusions from the posterity of a copper beech we must confine our attention to properly isolated trees.

In conclusion we may refer to the familiar fact that in cultivation mutations follow on one another so that the plant gradually becomes separated from the original form by an increasing number of characters; which is exactly what, in all probability, occurs in nature. The great number of long names of garden plants is evidence of this; as for example *Scabiosa atropurpurea nana purpurea* from which a *Forma carnea* and a *Forma rosea* have subsequently arisen; *Calliopsis tinctoria pumila purpurea, Tagetes patula nana* with dark leaves, and another form of this dwarf with bright yellow flowers and so forth. The succession of names often indicates the stages of development of the form in their historical sequence.

Finally, then, we may say that a gradual origin of elementary species has not yet been observed; but that there are hosts of instances in which new "species" have arisen suddenly or in which at least such an origin is in the very highest degree probable. Scarcely ever has the new form been isolated immediately it appeared: it is usually left like its parents to pollination by insects. So

far as this circumstance allows us to judge, these new species are as a rule just as constant as the older so-called "good" species.

§ 26. THE HYPOTHESIS OF INDISCRIMINATE MUTABILITY.

The chief merit of DARWIN's theory of selection was that it explained the adaptation which is seen on all hands in organic nature on purely natural principles and without the aid of any teleological conception. It is because it does this so completely that the theory of descent has gained such universal acceptance. The universal belief in the kinship of living forms, in its turn now makes the experimental study of the manner in which one species arises from another, possible. Nay, it challenges us to such an inquiry. How the species which exist at the present time arose in the past is evidently a historical question which can only be directly answered in a very few cases. But the determination of the mode of origin of species must soon become the subject of inquiry just like any other physiological process.

According to the Darwinian principle, species-forming variability[1]—mutability—does not take place in definite directions. According to that theory, deviations take place in almost every direction without preference for any particular one, and especially without preference for that direction along which differentiation happens to be proceeding. Every hypothesis which differs from DARWIN's in this respect must be rejected as teleological and unscientific.

The struggle for existence chooses from among the mutations at its disposal those which are the best adapted

[1] *Intracellulare Pangenesis*, pp. 73, 210, etc.

at the moment; in this way alone can their survival be explained.

According to WALLACE's and his followers' modification of the theory of selection that process concerns the individuals of one and the same species only. According to the theory of mutation, however, the units with which selection deals are the species themselves. Some survive and extend the limits of their distribution; others are wiped out; the former may again be the source of new species, the latter vanish and leave no posterity. The essential idea of this theory may be expressed by saying that by natural selection species are not *created* but eliminated.

WALLACE's theory of selection and the theory of mutation—specializations in two different directions of DARWIN's theory—both have to account for evolution without calling in the aid of a theory of variation in a definite direction. WALLACE's theory obviously does this inasmuch as according to it the material on which selection operates is individual variability; moreover the study of this variability rewards the student with a rich harvest of facts which might afford a strong support for this theory were there not other reasons for rejecting it.

The theory of mutation is in this respect less fortunate. For mutations themselves can only be directly observed in a very few cases; and in fewer still have they been properly studied. Mutations are naturally much rarer than individual variations, which every animal and plant exhibits; they do not lend themselves to investigation in the same way as the latter. Nevertheless they can be made the subject of research, and for many reasons they ought to be investigated just as minutely as variations have been.

One of the greatest faults of those who hold the current theories of selection is that they have focussed their attention much too exclusively on the phenomena of selection and individual variation and much too little on mutations. There can be no doubt that this is one of the chief causes of the depth of our ignorance of the facts of mutation.

This circumstance explains how it is that we can do no more in the matter of testing the hypothesis of indiscriminate mutability by the facts at our disposal, than find out how far the special hypotheses put forward by various authors are in harmony with fundamental and undisputed *Darwinian* principles.

Nor is this task an easy one. The question is obviously: what share in the origin of the larger or collective species is to be ascribed to mutability and what to the natural elimination of elementary species. Many authors have suggested that altered conditions of life exert a direct influence on animals and plants in such a way that new characters are developed which render their possessors better fitted to their new environment. The environment has, according to them, the power of directly evoking in the organism an adaptive response.

But this assumption seems to be no more than a begging of the question we are trying to answer. DARWIN's idea was that mutability took place in all directions and that the most favorable mutations were preserved. And this view of the matter will, it seems to me, remain the simplest and most probable answer to the question until such time as we have collected sufficient experimental evidence to decide whether this mutability exists or not.

We must now discuss in some detail the views of W.

B. Scott, one of the most prominent champions of the theory of mutation, who, however, has declared against the hypothesis of indiscriminate mutability on paleontological grounds. For it seems to me that this hypothesis agrees perfectly well with the facts of paleontology and especially with those wonderful genealogical series which have lately been discovered. Unfavorable species may well have arisen in far greater numbers than we should ever imagine, without having left the slightest trace in geological strata. The continuous series certainly point to selection in a constant direction during long periods of time, but by no means do they in my opinion demand a theory of mutability in a definite direction; for their explanation.

A closer examination of Scott's arguments will show how far my view is justified. Scott asserts that those paleontological series which are well known, are continuous and without gaps; whereas those in which the gaps are many are just those which are imperfectly known. This incompleteness is due either to the absence of individual strata from certain periods or to the fact that it has not yet been possible to examine the strata in question, properly. But where the series of strata is continuous and without gaps, and their examination thorough, the genealogical tree has also proved to be continuous and without gaps. This is evident in the case of the well-known pedigree of the horse, in those of many other mammals, of Ammonites and so forth.

Such series always possess this remarkable feature: they proceed, so to speak, in a straight line. Evolution makes straight for its goal without deviation, swerving

neither to the right nor to the left so as to form a zig-zag line.[1]

The question we have to answer now is how can such a definite and apparently predetermined series of changes be explained by natural principles and especially by the principles of descent enunciated by DARWIN; in other words: how must we picture mutability and natural selection to ourselves in order to gain a satisfactory explanation of these series. Two ways of explaining them are possible.

1. Mutability may take place in almost all directions; and it is natural selection which operates in one direction during long geological periods.
2. Mutability takes place only in one direction and itself determines the direction of change.

The former obviously represents the view of DARWIN; the latter that of SCOTT.

In the first place it must be remembered that when we are dealing with paleontological facts it is hardly possible to decide between mutability and selection, and, as SCOTT has remarked, no "explanation" can ever be much more than a guess.

There is every reason for supposing that in the genealogy of every organism numbers of species may have arisen but have never multiplied sufficiently to insure their preservation in the rocks, and have disappeared without leaving behind them either posterity or record. Paleontology can obviously not help us to decide as to the admissibility of such a theory. Let us therefore com-

[1] WELDON regards this objection to the theory of selection the most serious of all. See his Presidential Address: *On the Three Principal Objections which Are Urged Against the Theory of Natural Selection*, 8th Sept., 1898. Brit. Ass. Adv. Science, Bristol, 1899, p. 887.

pare the number of species in these geological series with the wealth of our modern collective species in elementary types. Can there be any question that this richness existed at all times in spite of the fact that there is no geological record of it?

We will again refer to the composite species *Draba verna*, which has been so fully elucidated by JORDAN, THURET, DE BARY, ROSEN and others. It is generally assumed that all the elementary species of *Draba verna* spring from a single original form; yet they differ from one another in every conceivable direction. They must have arisen as mutations from this form; which must therefore have produced them in all directions and not in one particular one. They afford sufficient material for natural selection; whatever view of it we hold.

Supposing that the ancestors of the horse exhibited a similar indiscriminate mutability, what chance would there be of their preservation in the fossil state? This question is a difficult one to answer and calls for further treatment. The present number of elementary types belonging to a species is no measure of the number of mutations it may have produced since its origin. By far the greater number of mutations presumably perish, nipped in the bud by natural selection. Other forms may continue for one or two years, but after a time, they too disappear. It is only a very few which ultimately come to take part in the great struggle for existence.

Much that appears, must forthwith disappear. Even between the male and female individuals of one and the same species there is often a strong competition which may result in a permanent alteration of their numerical proportions. As a rule male plants are more delicate, and we find quite regularly that in unfavorable positions

the females have increased in number in proportion to the males. This was observed by HOFFMANN on *Spinacia, Rumex* and *Lychnis,* and by others on many other species. In *Matthiola incana* the strongest seeds give double-flowered individuals but the proportions of such depend on the conditions in which they are cultivated; when seeds are gathered in the open they do not exceed 50%, when sown in pots they attain 60 and sometimes 70%.

It seems to me therefore to be a warrantable assumption that in geological times many newly arisen forms were promptly annihilated and have left no trace.

If the hypothesis of mutability in one direction renders the theory of a selection operating in a constant direction superfluous, then we must regard mutations as in a very high degree limited. Only those species, whose remains have been found in paleontological strata could have arisen by it; and strictly speaking only those which lay in the direct line of descent. All lateral branches which have died without posterity point to a selection operating continually in the direction of the main line of descent. It seems to me that the more we consider SCOTT's view in detail the more do the differences between him and DARWIN tend to disappear.

The question how far the theory that selection may have operated in one direction during long periods of time is justified lies outside the scope of this book: but it will be admitted first, that it has never been proved to be false, and secondly, that this theory has at least as much justification as that of mutability in one direction.

In short: *The mutation theory demands that organisms should exhibit mutability in almost all directions.* The facts of paleontology and classification are in accord

with this theory. And the fact that *ordinary or collective species consist of groups of elementary species whose characters may differ in every conceivable way emphasizes the existence of indiscriminate mutability.*

§ 27. THE HYPOTHESIS OF PERIODIC MUTABILITY.

The constancy of species is a demonstrated fact; their transmutability is still a matter of theory. This is the old objection against the theory of descent. LAMARCK, DARWIN and WALLACE met this difficulty by assuming that the immutability was only apparent and was due to the fact that the changes are so slow that in the short time during which we are able to observe them they can not be detected.

This however is merely an assumption, as I have already shown. No one doubts that many species have undergone vast changes during the course of centuries; but no one knows whether they have taken place gradually or by leaps and bounds.

The contrary supposition that species can remain absolutely unchanged during long periods of time but under certain circumstances begin to produce new forms seems to me at least equally justified. The ancestors of species that exist to-day have on this theory passed through immutable and mutable periods; the division of the large species into elementary species would be the result of the last or of some of the last periods of mutability.[1]

We repeatedly find the idea of a periodic transmutation of species expressed in DARWIN's works. "Changed

[1] KOLLMANN remarks on this subject: "In no species of animal or plant is this process—the formation of new races—a perpetual one but is confined to certain periods. If this were not the case we should have only changing forms and always new species instead

conditions of life" are the chief causes of this transmutation, and DARWIN cannot have imagined the environment to have been perpetually changing. Moreover DARWIN often refers to the fact that a plant exhibits little variability during the first few years after it has been brought into cultivation but after 3 or 5 years begins to give rise to new forms. Even if the explanation of this phenomenon should turn out to be different from that given by DARWIN, the fact that he insists so strongly upon it shows at any rate that the idea of periods of greater and of less mutability was present in his mind.[1] As the cause of these periods, DARWIN believed that external influences must act for many generations before they can induce any change of this kind.

But if mutability is a periodical phenomenon we get round the difficulty of having to suppose that mutations should appear equally at all times; and we are also in a position to account for the apparent periodicity in evolution. The existence of long intervals of time during which characters remain unaltered is, at any rate in the case of a great many species, a matter of tolerable certainty. The frequent, although not universal, existence of the same elementary species in localities which have been separated for centuries points decisively in this direction.

MORITZ WAGNER'S famous theory of migration is based on the same fundamental idea.[2] We have no reason to expect mutability so long as its external causes are absent. So long, that is to say, as the climatic, phys-

of the constant forms which actually exist." *Correspondenzblatt d. d. Ges. f. Anthropologie,* Vol. 31, No. 1, p. 3, Jan. 1900.

[1] "*I do believe that natural selection will generally act very slowly, only at long intervals of time.*" (DARWIN, *Origin,* 6th ed., p. 85.)

[2] WAGNER, *Das Migrationsgesetz der Organismen.*

ical and biological environment remains the same we must suppose that the species will not change. But if the plant extends its range, or if those with whom it competes for the means of subsistence, change in any way, the opportunity for the appearance of mutations is at once given. Either of these occurrences might result in a shorter or longer time in a rapid and considerable increase in the number of individuals and this might be the cause of the appearance of mutations on the scene. For a rapid multiplication of this kind presupposes the germination of such seeds as under ordinary circumstances either would not have germinated at all, or would have come to nought. This might be the case for example with seeds of weak lateral branches, of the tips of inflorescences or of flowers from accessory buds and so forth.

But these are after all only suggestions; and I feel strongly that we ought to make this matter a subject for experimental inquiry; to look for species which happen to be going through a period of mutation and still more to discover what are the factors which will enable us to induce such a period in a species at will. We have a doctrine of descent resting on a morphological foundation. The time has come to erect one on an experimental basis.

§ 28. THE PHENOMENON OF MUTATION WITHIN THE LIMITS OF THE MUTATION PERIODS.

Observations on periods of mutation have not yet been made. On the other hand many attempts based on *a priori* considerations have been made to discover what the phenomenon of mutation may be expected to be like.

Two theses, which help to remove many difficulties standing in the way of the mutation theory, have been put forward:

1. The assumption that the new form or species does not arise merely once from the parent species but, while the period lasts, a great many times and with some degree of regularity.
2. The possibility of the appearance of useless or even harmful specific characters—whose existence is not compatible with the ordinary theory of selection.

The object of these considerations was to show that newly arisen forms could increase sufficiently to enter the struggle for existence with at any rate a fair prospect of success, without the help of natural selection. But the fact that the actual behavior of new forms when they arose was insufficiently known and that arguments therefore could not start from *a posteriori* premises had the result that this subject received little attention. GULICK and DELBOEUF are the two chief writers who have devoted themselves to this aspect of the question.

GULICK's generalization was: *An initial tendency due to accidental variation can increase and develop in succeeding generations, without reference to the advantage of the species.* He is referring not to an extreme variant of individual variation but to a mutation; and moreover to one on which natural selection, at first at any rate, has no effect.[1]

J. DELBOEUF is concerned to show how the final usurpation, by the transmuted forms, of the space and means of subsistence which supported the original type is a

[1] See *Journ. Linn. Soc. Zool.*, Vol. XI, p. 496 and Vol. XX (1888) p. 215.

necessary consequence of the continuation of the cause, which gave rise to the first deviation, however slight it may have been.[1]

A sharp distinction between the selection and the mutation theory was not drawn at the time when DELBOEUF was writing, so that his attention was directed indiscriminately to both of them. I shall consider the application of DELBOEUF's thesis to the latter only. And I shall further limit my analysis to the consideration of those cases in which the new form is immediately constant, and this, as we saw in § 25, is almost always the case.

DELBOEUF starts with the supposition that a mutation does not arise only once but is given off every generation in a definite although perhaps a small number of individuals for just so long as the cause of the mutation continues. He further supposes that the new form can multiply in peace, and that its increase is neither aided nor hindered by the struggle for existence. Under these conditions the new form must always increase in number of individuals in relation to the parent form with a speed which will vary directly with the percentage of mutating individuals produced in each generation. From a knowledge of this percentage one could calculate the number of generations it would take for the new form to equal the old one in number, and also how many years must elapse before the new form entirely replaces its progenitor.

In the numerical tables of DELBOEUF's paper some of the more important cases are worked out in detail. The general principle, however, is quite clear: *A new*

[1] J. DELBOEUF, *Ein auf die Umwandlungstheorie anwendbares mathematisches Gesetz,* Kosmos, 1877-1878, Jahrg. I, Bd. II, pp. 105-127, especially p. 112.

form without any advantage whatsoever in the struggle for existence will maintain itself provided (1) that it is sufficiently vigorous and fertile and (2) that it does not arise merely once but repeatedly during a long period of time.[1]

DELBOEUF'S generalization has received little attention. Nevertheless it seems to me, in principle and in the light of the facts of mutation, to be sound. It explains in a very simple way the existence of the vast number of specific characters which are quite useless or at any rate as to the use of which we have no idea at all—as for example the differences between the oft-cited species of *Draba verna.*

According to the commonly accepted theory of selection only characters advantageous to their possessors should arise; according to the theory of mutation on the other hand useless and even disadvantageous ones may also appear. And according to DELBOEUF'S view, the latter may also persist through long intervals of time side by side with the useful variations. The premises from which he starts are at any rate warranted by actual experience.

[1] With regard to the probability of this last condition I refer the reader to the instances in § 25, pp. 193-196, and to the repeated appearance of sterile maize (in my experiments) both of which support this view.

VI. CONCLUSION.

1. The student of morphological and historical evolution is concerned with the origin of the Linnean or collective species, genera, families and larger groups. The student of experimental evolution is concerned with the origin of elementary species, or rather with the origin of specific characters.

2. "The real difficulty of DARWIN's theory is the transition from artificial to natural selection" (PAUL JANET). This difficulty can only be surmounted by admitting that the improvement of races and the origin of new forms are really entirely different, and only apparently similar, processes.

In DARWIN's time no distinction was drawn between these two processes.

3. "No two individuals in a generation are absolutely alike." This well-known saying refers to fluctuating variability and has nothing to do with the theory of descent.

4. "Species have arisen by natural selection resulting from the struggle for existence." This statement also needs some explanation. The struggle for existence, that is to say the competition for the means of subsistence, may refer to two entirely different things. On the one hand the struggle takes place between the individuals of one and the same elementary species, on the other between the various species themselves. The former is a

struggle between fluctuations, the latter between mutations. In the former case those that survive are the individuals which find conditions favorable to them—that is to say, as a rule, the strongest individuals. It is by this process that local races arise, and by it that acclimatization is rendered possible. If the new conditions of life are relaxed, the adapted race reverts to the form from which it sprang.

The natural selection of newly arisen elementary species in the struggle for existence is an entirely different matter. They arise suddenly and without any obvious cause; they increase and multiply because the new characters are inherited. When this increase leads to a struggle for existence the weaker succumb and are eliminated. According as the young or the parent form is better fitted to the environment will the one or the other of them survive. Species no more *arise* as the result of this struggle for existence, than they do as the result of the struggle between the variants of one and the same type—though for different reasons in the two cases. In order that species may engage in competition with one another it is evidently an essential condition that they should already be in existence; the struggle only decides which of them shall survive and which shall disappear.

It is evident moreover that this "elimination of species" must have weeded out many more than it has preserved.

In a word, from the standpoint of the theory of mutation it is clear that the rôle played by natural selection in the origin of species is a destructive, and not a constructive one.

5. Herbert Spencer's well-known expression: "The survival of the fittest" may mean one of two things:

either (1) the survival of the most favorable individuals within the limits of the constant species or in the formation of local races or (2) "*the survival of the fittest species*" as the basis for the theory of descent. The two expressions are quite independent of one another and refer to two entirely different spheres of inquiry.

6. According to the theory of mutation species have not arisen gradually as the result of selection operating for hundreds, or thousands, of years but discontinuously by sudden, however small, changes. In contradistinction to fluctuating variations which are merely of a *plus* or *minus* character the changes which we call mutations are given off in almost every manner of new direction. They only appear from time to time, their periodicity being probably due to perfectly definite but hitherto undiscovered causes.

The theory of the inheritance of acquired characters comes under the heading of fluctuations. Acquired characters have nothing to do with the origin of species. Nor can the theory of descent be applied to the solution of social problems.

PART II.

THE ORIGIN OF ELEMENTARY SPECIES IN THE GENUS OENOTHERA.

I. THE PEDIGREE FAMILIES.

§ 1. OENOTHERA LAMARCKIANA, A MUTATING PLANT.

(PLATE I.)

The chief obstacle in the way of getting material suitable for investigating the origin of species is our complete ignorance of the conditions under which this process takes place. In order to obtain this material I started in 1886, to search the country round Amsterdam for species, exhibiting such monstrosities or other peculiarities as I thought would suit my purpose. As a result of my quest I brought over one hundred species into cultivation, but only one of these turned out to be what I really wanted.

From this I conclude that most of the species in this locality are passing through a period of non-mutation, and that plants which happen to be actually passing through a mutable phase are encountered at any rate, relatively rarely.

The plant in question is *Oenothera Lamarckiana*, which together with its nearest allies *O. biennis* and *O. muricata* have been introduced into Europe from America. The species *Lamarckiana* differs from the others by its taller growth, by its much larger and more beautiful flowers, by the fact that self-fertilization rarely occurs, by its different leaves, and so forth.[1] *O. La-*

[1] For the synonyms, and a discussion of the relationship as well as for a more detailed account of its origin see *Sur l'introduction de*

marckiana was introduced from America into our gardens, from which it has subsequently escaped. At any rate this was the case in the locality in which I found it.

This was close to Hilversum and afforded peculiarly favorable circumstances for the most minute investigation. I visited the place during the summers of the years 1886-1888 almost every week, and, since that date at least once or twice nearly every year. The plant grew in a

Fig. 42. *Oenothera Lamarckiana.* A flower nearly natural size. One of the petals has been removed to show the eight stamens with the pistil and its stigma.

disused potato-field to which it had spread from a neighboring park. It began to spread in about the year 1875, and during the 10 years 1875-1885 it extended over about half the field. In the succeeding years it multiplied still

l'Oenothera Lamarckiana dans les Pays-Bas, in *Nederlandsch Kruidkundig Archief,* T. VI, 4, 1895; also the later sections of this Part.

more rapidly; until the field was finally planted with forest trees. At the present day traces of the plant still exist.

A rapid multiplication of this kind during the course of a relatively short period of time has often been considered as one of the conditions for the appearance of a mutable period. This consideration led to a closer investigation on the spot, which confirmed the conclusion.

The plant exhibited a high degree of fluctuating variability in all its organs and characters. It presented also numerous variations of another kind, of which I shall only mention fasciation[1] and "pitcher"-like malformations.[2] Most of the plants were biennials, but many were annuals; and a few lived three years, as in the case of the beet.

That I really had hit upon a plant in a mutable period became evident from the discovery, which I made a year later, of two perfectly definite forms which were immediately recognizable as two new elementary species. One of them was a short-styled form: *O. brevistylis,* which at first seemed to be exclusively male, but later proved to have the power, at least in the case of several individuals, of developing small capsules with a few fertile seeds. The other was a smooth-leaved form with much prettier foliage than *O. Lamarckiana* and remarkable for the fact that some of its petals are smaller than those of the parent type, and lack the emarginate form which gives the petals of *Lamarckiana* their cordate character. I call this form *O laevifolia.*[3]

[1] *Over de erfelykheid der fasciatiën. Kruidkundig Jaarboek Dodonaea,* 1894, p. 72. Cf. pp. 92-95.

[2] *Over de erfelykheid der synfisen.* Ibid., p. 129. Cf. p. 165.

[3] Both forms are described and, in part, illustrated by Prof. Julius Pohl: *Ueber Variationsweite der Oenothera Lamarckiana,* in

Both *O. brevistylis* and *O. laevifolia* come perfectly true from seed as will be shown later on. They differ from *O. Lamarckiana* in numerous characters, and are therefore to be considered as true elementary species.

When I first discovered them (1887) they were represented by very few individuals. Moreover each form occupied a particular spot on the field. *O. brevistylis* occurred quite close to the base from which the Oenothera had spread; *O. laevifolia* on the other hand, in a small group of 10 to 12 plants, some of which were flowering whilst others consisted only of radical leaves, in a part of the field which had not up to that time been occupied by *O. Lamarckiana*. The impression produced was that all these plants had come from the seeds of a single mutant. Since that time, both the new forms have more or less spread over the field.

I could find neither of these forms in the herbaria of Leiden, Paris or Kew; nor have they, so far as I have been able to discover, been described from other localities. Whether or no they did arise in my locality can of course no longer be determined. But I think that until proof to the contrary is forthcoming this must be regarded as extremely probable. So much at any rate is certain that the discovery of these two species increased my hope of witnessing the origin of other species from the same stock—a hope which was soon to be fulfilled.

In the autumn of 1886 I brought two samples from Hilversum to Amsterdam for cultivation in the experimental garden. One lot consisted of nine particularly fine rosettes with almost fleshy roots; the other, of the seed from a quinquelocular fruit from a plant growing

Oesterr. Botan. Zeitschr., 1895, Nos. 5 and 6. (*O. laevifolia* is referred to there as *O. oxypetala*).

in the middle of the field. Lastly, in the autumn of 1887 I collected the seeds of *O. laevifolia*. I obtained in this way three groups which, in conformity with the principle of nomenclature adopted by growers of beets, I call families; and these I continue to grow, separately, to the present day.

From these three families and their numerous lateral branches I have derived my whole culture, which has embraced several thousands of individuals almost every year. Latterly several hundreds of plants have been artificially fertilized for seed purposes every year.

Furthermore I have imported *O. brevistylis* direct from Hilversum, because it did not arise in my cultures. I have also occasionally made collections of seed in the field to afford material for control experiments.

In each of these three families new species have arisen in my garden; and they have been essentially the same in the three groups. I shall deal with them separately: first with that derived from the rosettes, the progeny of which I shall call the *Lamarckiana*-family. Of this family the main trunk (§ 2) and a lateral branch (§ 5) will be dealt with separately, for the sake of simplicity of treatment; but the results arrived at with the latter agree, in their broad features, with those obtained from the former.

From the seeds of *O. laevifolia* the *Laevifolia*-family (§ 6) arose; from the seeds of the above-mentioned fruit a group which I shall call the *Lata*-family.

§ 2. THE LAMARCKIANA-FAMILY.

The original parents of this family were, as we have already seen, moved to the botanical garden in Amsterdam in the autumn of 1886. They flowered in 1887,

bearing large blossoms both on the main stem and on the numerous lateral branches, and set a quantity of seed. They were grown on an isolated bed and considered as the first generation.

From their seeds I raised, in 1888 and 1889, a second generation which flowered on the same isolated bed. I chose six of the strongest to gather seeds from. The third generation was mature in 1891; it was not isolated, but flowered in that year before the other cultures of *Oenothera* began to bloom; some days before this happened all open flowers and all the buds were removed.

From the seeds of the first and second generation there appeared, besides the normal plants, three hitherto unknown forms: *O. nanella* and *O lata* in some numbers, and a single example of *O. rubrinervis.*

My hope had been fulfilled. But the difficulties of the experiment had meanwhile become so great that I was obliged to give it up for a time. The *laevifolia*-family was meanwhile continued and experiments in methods of cultivation, manuring and artificial fertilization and so forth were carried out on a large scale. The result was that in 1895 I was able to take the *Lamarckiana*-family up again with results which far exceeded my highest expectations, as a glance at the genealogical tree on page 224 will show. Since that time I have manured my plants heavily, isolated any mutating individuals as soon as they could be recognized as such and have then chosen the strongest rosettes, as early as possible, as seed-parents for the next generation. I have, further, treated my plants as much as possible as annuals; and have always chosen those which were to produce seed for the next generation in the main line from among these. So that from 1895 to 1899 I always had one generation

each year. Fertilization was always artificial; the flowers set plenty of seed when impregnated with their own pollen. The visits of insects were precluded by the use of prepared paper bags.[1] The production of new species has not in the least suffered from all these precautions.

I shall now summarize the whole history of this family in the form of a genealogical tree (p. 224), including in it only the main line of descent and the individuals which mutated directly from it.

The table shows the eight generations in succession; the first 1886-1887, consists of the nine plants collected in the field at Hilversum; this and the two following generations each occupy two years. I did not sow the seeds which I harvested in 1891 till 1895; from that time on, each generation occupies only a year. In the column over which *O. Lam.* is written are given the approximate numbers of individuals which were examined either as seedlings or as grown plants, in each year. These numbers do not refer to the total number of seeds sown or even to the number of seedlings that came up, but to plants which were examined separately.

The table also shows the number of plants which mutated in each generation, so far as they could be recognized with certainty. It is probable that these numbers are in many cases too small because I had not nearly space enough to grow all the seedlings separately until they had so far grown that their true character was a matter of absolute certainty. They had as a rule to be examined as seedlings and it is probable that in this way many cases of mutation were overlooked.

I have only recorded the more important mutations

[1] *"On the Use of Transparent Paper Bags for Artificial Fertilization,"* in *Hybrid Conference Report*; Journal Royal Horticultural Society, Vol. XXIV, April 1900, p. 266.

OENOTHERA LAMARCKIANA.

A

THE LAMARCKIANA FAMILY.

I

TABLE SHOWING THE ORIGIN OF NEW SPECIES FROM THE TYPE.

(The figures refer to the numbers of individuals.)

GENERATIONS		SPECIES							
		gigas	albida	oblonga	rubrinervis	Lam.	nanella	lata	scintillans
VIII	8th gen. 1899 (annual)		5	1	0	1700	21	1	
VII	7th gen. 1898 (annual)			9	0	3000	11		
VI	6th gen. 1897 (annual)		11	29	3	1800	9	5	1
V	5th gen. 1896 (annual)		25	135	20	8000	49	142	6
IV	4th gen. 1895 (annual)	1	15	176	8	14000	60	73	1
III	3rd gen. 1890-91 (biennial)				1	10000	3	3	
II	2nd gen. 1888-89 (biennial)					15000	5	5	
I	1st gen. 1886-87 Hilversum and Amsterdam (biennial)					9			

in the table: others have arisen, but they have either not flowered or, being partially sterile, have set no seed; or are of minor importance for other reasons. As examples of such we may just mention *O. sublinearis* and *O. subovata* and two or three allied types, which could not be distinguished with certainty because they bore no seed. From others as, e. g., *O. leptocarpa, O. elliptica,* and *O. semilata* I have made sowings with successful results although the experiments were carried out on a small scale (cf. §§ 16-20). In the case of one form, *O. spathulata,* I have so far only obtained rosettes, and the same is true of other forms to which I do not propose to give special names.

The above-mentioned *O. lacvifolia* and *O. brevistylis,* which were found in the original locality never appeared in my cultures.

The numbers on the table show that my experiment dealt in seven generations with about 50,000 plants and that of these over 800 mutated; i. e., about 1.5%, a figure which must for many reasons be regarded rather as too small than too large. In the case of every mutated individual it is certain that since 1886 its ancestors were normal *O. Lamarckiana.*

Whether this was the case with the earlier ancestors is obviously now beyond the range of proof, but it may be assumed to have been so with a great degree of probability because of the extreme rarity of forms that showed any deviation in the field at Hilversum.

§ 3. THE MUTATIONS IN THE LAMARCKIANA-FAMILY.

I shall now describe the mode of origin and the more important characters of the seven new species mentioned in the table.

I. *O. gigas.*[1] A vigorous plant with broad leaves, large flowers and short fruits and, so to speak, better in habit than *O. Lamarckiana* in every respect. It has the appearance of being just as well fitted for the struggle for existence as any species of the genus to which it belongs.

Even the radical leaves of quite young plants betray the identity of the new type. They are broad with a broad base which passes into the petiole abruptly instead of gradually as in the case of *Lamarckiana.* The leaves that appear later possess this character in a less degree, but it is always recognisable. The form of the leaf is moreover very much more variable than in any other form of the subgenus *Onagra*; examples with very narrow and others with very broad leaves occur in quite small groups of individuals.

Its stem is thicker than, though about the same height

[1] With regard to the nomenclature it must be mentioned that my plants are burdened with a formidable series of synonyms from the very moment that they appear. Some authors regard *O. Lamarckiana* as a variety of *O. biennis.* Others separate the subgenus *Onagra* as a distinct genus. *O. gigas* has therefore the following equally legitimate synonyms:

O. gigas.
Oenothera Lamarckiana gigas.
Oenothera biennis gigas.
Oenothera biennis Lamarckiana gigas.
Onagra gigas.
Onagra Lamarckiana gigas.
Onagra biennis gigas.
Onagra biennis Lamarckiana gigas.

The same is true of the other new forms. It may also be noted that *Oenothera* is written by many authors *Onothera,* whilst *Lamarckiana* may be written *lamarckiana* or *Lamarkiana.*

as that of *O. Lamarckiana.* It is much more densely clothed with foliage than the parent form, a state of affairs brought about by the fact that the nodes are closer together and that the leaves hang down.

The inflorescences are extraordinarily luxuriant, with short internodes, broad bracts and very large flowers which form a much fuller and more beautiful group than those of *O. Lamarckiana.* The fruits are short and thick and more or less conical; the seeds are very large.

In spite of the high degree of variability which this plant exhibits it can be distinguished with ease from its relatives at every stage of its development.[1]

This species arose only once in the *Lamarckiana*-family as the table on page 224 shows. In the other families it has also only appeared twice.

Its appearance was on this wise. In 1895 I had a crop of about 14,000 plants constituting the 4th generation of the *Lamarckiana*-family. All the mutated individuals had been transplanted from this crop, and the majority of the *Lamarckianas* had been weeded out, to give more space to those which were to provide seed for the next generation. At the beginning of August I had about 1000 of these plants in flower, but many were still in the rosette stage. I chose 32 of the strongest and finest of these rosettes and planted them in a separate bed the proper distance apart.

These plants grew up the next year and flowered in July and August. One of them caught my eye with its thick stem, rather compressed inflorescence and noticeably larger flowers. On the 10th of August I picked off all the flowers, both the open ones and those which were

[1] For a more detailed description of this and the other new species see the next chapter.

through blooming, enclosed the inflorescence in a paper bag; and, later, fertilized the flowers myself with their own pollen. The plant set a quantity of seed; the fruits were short and thick, the seeds large.

This plant was the parent of the new species *O. gigas*. Its ancestors were at least for three generations ordinary *O. Lamarckiana*. The new form arose without any intermediate stages or previous warning; it is so striking when in flower that it could not have been overlooked if it had existed before. And it must be remembered that the number of seed-bearing plants in each of the three generations were respectively only 9, 6 and 10, and that they were under continual and close observation.

The self-fertilized seeds of the original plant of *O. gigas* were sown separately in 1897. They gave rise to somewhat over 450 plants. All of them proved to be like their parent and constituted without any question a type distinct, from the very outset, from *O. Lamarckiana*. Only one plant did not conform to this type; it had all the characters of *O. gigas,* but possessed the dwarf habit of *O. nanella*. It will henceforth be referred to as *O. gigas nanella*. Not a single one of the 450 plants reverted to *O. Lamarckiana*.

Lack of space prevented me from keeping more than a quarter of this crop till the end of the summer. Many stayed in the rosette stage, others produced stems and flowered; all were pure *O. gigas*. I saved seed from some of these plants whose flowers had been covered with paper bags and self-fertilized.

This experiment proves that this species was perfectly constant from its very first appearance. And it remained so for the three subsequent generations.[1]

[1] And afterwards, until now (Note of 1908).

We may postpone further details of this case to a later section and proceed to the following generalization as being fully warranted by the evidence.

A new elementary species can appear without any obvious cause in a single individual and be absolutely constant from the very outset.

As I have already stated this form has appeared twice again in my experiments.

II. *O. albida.* A pale green, rather brittle, and very delicate form with narrow leaves; never attaining anything like the height of *O. Lamarckiana* and bearing pale flowers and weak fruits which contain little seed.

It appears every year in most of the cultures in larger or smaller numbers; as a young rosette it is immediately recognizable. They are so weak that in the first generations I imagined them to be diseased and did not record them; that is the reason for the absence of any mention of their occurrence in the years 1888 and 1890 in the table on page 224.

In spite of their frequent appearance it was not till 1896 that I could get one of them to flower. I mention this in order to allay any suspicion that crossing may have been the cause of their repeated appearance, before the 6th generation.

All that remained of the 1895 crop in 1896 was a single plant, which was consequently biennial. A few isolated flowers appeared on it but they bore scarcely any pollen and set no seed after I had fertilized them with their own pollen and covered them with a paper bag.

In 1897 however I succeeded in getting five biennial plants to flower; and in obtaining seed from them after artificial fertilization. From these seeds I raised a

second generation in 1898 and a third in 1899, both of annual individuals. Both generations were absolutely constant and exhibited no signs of reversion; but consisted only of a few individuals on account of the paucity of the harvest which each generation gave (86 in 1898 and 36 in 1899).

III. *O. rubrinervis.* A beautiful species which often has red veins on the leaves and broad red stripes on the calyx and fruit. Markings of this kind do, it is true, occur sometimes on *O. Lamarckiana,* but they are never so pronounced that their possessors could possibly be mistaken for *O rubrinervis.* The flowers are somewhat larger and a rather darker yellow. The stem, especially in annual cultures, is generally shorter than that of *Lamarckiana* and suffused with red. The species cannot as a rule be recognized in the very young rosette stage;[1] in fact not till the plant has 10-20 leaves, or later if the plants are grown too close together. *Rubrinervis* was therefore not detected until after the *latas* and *nanellas* had been identified and removed. It is then easily recognizable by its narrow and long leaves with red veins, and by its vigorous habit.

A very peculiar feature of this species is the brittleness which characterizes the annual forms to a much greater extent than the biennial ones. The stem and leaves can be broken by a moderately hard blow. If such a blow is administered to the flowering plant from above, the stem splits into several pieces with perfectly smooth surfaces of fracture. The cause of this is the extraordinarily slight development of the bast-fibres which however are not entirely lacking as microscopical investi-

[1] The distinguishing characters have since been found in very young seedlings (Note of 1908).

gation shows. If a fruit is pulled off without great care the stem is usually broken in the process, an event which has more than once caused me considerable annoyance at harvest time.

In all its other characters *O. rubrinervis* is a very healthy plant—quite as strong as *O. Lamarckiana* at any rate. It is the only one of my new species which is not inferior to the parent type in richness in pollen and seed. Apart from its brittleness it seems to be fully qualified for the struggle for existence. I have not however yet organized any experiments to determine this point.

O. rubrinervis appeared in the main line of descent, as the table on page 224 shows, in the third, fourth, fifth and sixth generations. There were 32 examples of it altogether. In the other families it was also observed from time to time; and appeared as early as 1889 in the *lacvifolia*-family. In 1897 only three appeared in the main line of the *Lamarckiana*-family, whilst 10 appeared in the branch lines of descent. Their ancestors for at least five generations back were all *O. Lamarckiana*, or at least not of the *rubrinervis* type.

O. rubrinervis appears each time without visible preparation: and what strikes one most is the absolute constancy of the characters although these were quite distinct from those of its ancestors.

When once I recognized a plant in its rosette stage as being a *rubrinervis* I could predict that it would have a fragile and brittle stem and red calyx and fruit. This constancy in character is a feature of all my new elementary species and is even more striking in the case of *O. lata* than in *rubrinervis*.

I first started experiments on the constancy of the new *rubrinervis* in 1896 and 1897. In 1895 I covered

the eight individuals which appeared in that year and fertilized them with their own pollen, (see table on page 224). From the seeds thus obtained I raised a considerable number of plants in 1896; the seeds were sown in pans and all the seedlings picked out onto a bed. With the exception of a few that were to serve as seed-parents, they were all pulled up while they were flowering (from August to October) i. e., not before the time when the *rubrinervis*-character was fully developed in the stalk, calyx, flower and young fruit. There were some young stems and rosettes left over after this process, but these also proved to be examples of *rubrinervis*. The number of plants that flowered amounted to about 1000. Among these was a single *Lamarckiana* which had presumably grown from a seed left in the bed from last year's sowing. Otherwise all the plants were *rubrinervis*; except that some of them also exhibited the

Fig. 43. *Oenothera rubrinervis.* Top of the plant, showing flowers, buds, and unripe fruits.

features of *Oenothera leptocarpa,* a new species at that time.

The existence of the single *Lamarckiana* was plainly a difficulty, so that I not only continued but repeated the experiment.

For the continuation of the experiment I used the seeds saved in 1896. I raised from them, in 1897, 1114 plants; every single one of which was a *rubrinervis.*

For the repetition of the experiment I used the self-fertilized seeds of the four plants which had arisen in 1896 from the *Lamarckiana*-family and could therefore boast four generations of pure *Lamarckiana* ancestry. From these seeds I raised altogether 1862 plants, which were without exception *rubrinervis.*

Fig. 44. *Oenothera oblonga.* Upper part of a plant at the commencement of flowering.

From these facts I conclude:

1. That *rubrinervis* is an absolutely constant elementary species.

2. That every example of *rubrinervis* that arises in a family of another kind is capable of producing perfectly constant progeny.

IV. *O. oblonga.* The seedlings of this species can first be recognized as such at the appearance of about the sixth leaf, that is a little after *O. lata* and *O. nanella* and considerably earlier than *O. rubrinervis* and *O. scintillans.* The leaves are narrow and with long stalks; the transition from the leaf to its stalk is not gradual but abrupt, and the broad and pale veins have a reddish tinge underneath. *O. oblonga* can only be recognized uniformly early when the plants among which it appears are grown sufficiently far apart, but if the undoubted examples of *oblonga* are removed from time to time more examples of it will be found as a result of the additional space put at the disposal of the plants.

The typical form of the leaf, to which we have referred, was maintained in the rosettes that were planted out. Some of the plants bore stems in the first year, others turned out to be biennials. In both cases the plants reach a moderate height only, rarely attaining a meter in height and being very much smaller than plants of *Lamarckiana* grown under identical conditions. The annual forms branch but little, and the branches themselves remain short. The terminal spikes are thickly covered with flowers and buds; the flowers themselves are smaller than in *O. Lamarckiana* and develop small fruits which contain very little seed. The biennial forms branch more, and bear plenty of pollen; they form short but stout fruits which contain abundance of seed.

Towards the end of their flowering period the *oblonga* plants can be recognized from quite far off by the

way in which their small unripe fruits are crowded together.

In the fourth generation of my *Lamarckiana*-family (grown in 1895 and consisting of 14,000 plants) there were 176 *O. oblonga*; in the fifth generation (grown in 1896 and consisting of 8000) there were 135. That is, in the one case 1.3, in the other 1.7 %. In the sixth generation this proportion was maintained (*29* in 1800 = 1.6%). In the last two the number has been much smaller because the counting had to be discontinued too early.

In 1896 I got seeds from biennial plants of the fourth generation, and from annual ones of the fifth by artificial self-fertilization in paper-bags. There were seven of the biennial seed-parents: each of them produced between two and three hundred seeds which were sown in separate lots. Altogether 1683 plants were raised from them. They were all *oblonga* with the exception of one which had the characters of *albida*. There were no examples of *Lamarckiana* among them.

Ten of the annual plants of the fifth generation set seed which was, however, scanty and germinated badly. Only 64 plants were raised; of these one was *O. rubrinervis*, the rest *oblonga*. There were no *Lamarckianas*.

I have tested the constancy of other examples of *oblonga* which have arisen in other families with the same result.

Oenothera oblonga is, therefore, perfectly constant directly it arises, but it has the power of, itself, giving rise to new forms.

V. *O. nanella* (*O. Lamarckiana nanella*). Dwarf *Oenothera*. We are not now concerned with the question whether a particular form is to be described as a spe-

cies or as a variety. Our business is to test its constancy by experiment. But the result of this will not help us to decide between species and variety.

Fig. 45. *Oenothera nanella.* A thinly and a densely leaved individual on one of the first days of the flowering period. The plants were about 15 and 20 cm. high, whereas annual plants of *O. Lamarckiana* begin to flower when they are about one meter high.

If a form proves to be constant but is distinguished from another form only by a single character, it is re-

garded by most authorities as a variety; and this is especially the case with dwarf forms, which are known for a whole series of species, and attain only half or less of the stature of the species to which they belong.

On this ground *O. nanella* may be regarded as a variety; but it must not be forgotten that, from the experimental point of view, it is just as good an elementary species as those which we have described already.[1]

The dwarfs are, perhaps with the exception of *O. lata,* the easiest to recognize in my cultures. They appeared annually, in every culture, except the smaller ones. Among the 50,000 individuals which composed the whole *Lamarckiana*-family, 158 were *nanella*; that is about 0.3%, a proportion which was remarkably constant in successive years.

The dwarfs can be easily and certainly recognized during the whole course of their development. If grown far apart and well lighted they are recognizable as soon as the second leaf appears; the first leaf is, at that time, broad with a broad almost heart-shaped base closely set on its short petiole. In 1897 I identified and recorded them by this character. Plants about which there was the slightest doubt were allowed to develop further.

The broad stumpy leaves are succeeded by one or two lozenge-shaped ones with long stalks; and the plant looks as if it were reverting to *O. Lamarckiana.* This however is not the case, for there soon follow a number of very broad leaves, with very short petioles, closely crowded together; with the result that the highly characteristic dwarf rosette is formed. The way I dealt with these plants in 1896 was to plant them out after

[1] Jordan, (*De l'origine des arbres fruitiers,* 1853) has pointed out that varieties are only a special form of elementary species.

the second leaf had appeared in well manured soil and at a good distance apart. They were about 6 weeks old when I finally identified them.

The rosettes nearly always bore a stem in the first year; I only obtained biennial plants by sowing the seed late or by crowding. The biennial form is richly branched; the annual has very few lateral branches (Fig. 45). The internodes are numerous and very short, the broad short-stalked leaves are therefore much crowded.[1] The petioles are brittle. The first flowers often open when the plant has scarcely reached a height of 10 centimeters; after their first appearance flowers are usually born at regular intervals but sometimes sporadically. The flowers are almost as big as those of *O. Lamarckiana*; so that the plant in flower is very showy. The fruits are not perceptibly smaller than those of the parent species.

In order to protect the first flowers from the visits of insects I enclosed the whole plant in a bag of parchment, the margin of which is attached to a metal ring which is firmly pressed into the ground. It is not until the inflorescences have attained a considerable length that the flowers can be enclosed in parchment bags in the ordinary way.

The first dwarfs I fertilized in this way were some which flowered in 1893. Their ancestors which had not been protected from the visits of insects and only incompletely isolated had notwithstanding this, already exhibited a high degree of constancy. The seeds collected in 1893 gave rise to 440 seedlings which were all *nanella*.

In 1895 I self-fertilized a series of dwarfs which arose in the fourth generation of my *Lamarckiana*-family

[1] The characteristics of the dwarfs are in part due to a disease; see § 18 (Note of 1908).

and had therefore at least three generations of ancestors with the normal high stature. In the same year I also sowed some seed saved from the second generation (1888-1889) and I self-fertilized some of the dwarfs that appeared in the crop thus raised. There were altogether 20 of them; they set a quantity of seed from which 2463 seedlings were grown. They were without exception *O. nanella.*

Thus we see that every one of the twenty dwarfs which arose spontaneously from *O. Lamarckiana* had a perfectly constant progeny. As I have already stated, the plants were not registered as dwarfs until they were strong rosettes and had attained the age of about six weeks.

I repeated the experiment on a larger scale in the following year, when I had found out how to identify the plants without transplanting them. I used the seeds of *nanella* plants which had arisen in the fifth generation of the *Lamarckiana*-family, i. e., plants whose ancestors had therefore been normal for four generations. From the seeds of 36 plants I raised over 18,000 seedlings. These were without exception *nanella*; but 3 of them exhibited in addition to the dwarf habit the characters of *O. oblonga* and constituted an elementary species of the second grade, *O. nanella oblonga.*

Moreover, whenever *nanella* appeared in other families it proved immediately constant, not only in the first but in succeeding generations as well.

Combinations with other characters occurred in these cultures; but very rarely. I have often had examples of *O. lata nanella* and *O. nanella elliptica,* and now and again variegated or pitcher forming individuals of *O. nanella,* and so on.

VI. *O. lata.* This species is solely female; it never

forms the slightest trace of pollen.[1] With the pollen of *Lamarckiana* or any of its deviations it is perfectly fertile and gives a proportion of *lata*-plants which varies about 15-20 %.

Julius Pohl has investigated the cause of its sterility.[2] The pollen sacks of the open flower are dry to the touch; they seem to be empty, but as a matter of fact contain a little pollen which is seen under the microscope to consist of empty grains which are not merely poor in protoplasm but shrivelled and stunted. The development of the anthers is at first normal, up to the formation of tetrads. About this time the surrounding cells of the tapetum elongate; and subsequently grow into the cavity of the sack. These cells disappear at a later stage, when the pollen grains may be found lying in the mucus which they leave behind.

I spent a great deal of time in transferring these scanty masses of pollen to the stigma in the hope of obtaining a few seeds if possible, but all in vain. If the visits of insects were prevented the plants set no seed.

The exclusively female character of this mutant is very important, for it shows in a most direct way that the remarkably regular production of *O. lata* year after year in the *Lamarckiana*-family cannot be due to accidental crossing—an explanation of the frequency and regularity of its appearance which is also disproved by

[1] Of late I have discovered a hybrid strain of *lata* which produces pollen in a greater or smaller part of its flowers. These plants, when self-fertilized, produce seed, which gives 15-20 % examples of *lata*, and 80-85 % of *Lamarckiana*. Also the same figures as by pollination with the parent-species. This proves the *O. lata* to be an inconstant species. Seeds of this strain have been distributed to some of my correspondents, who also found the type to be inconstant.—(Note of 1908.)

[2] Julius Pohl, *Ueber Variationsweite der Oenothera Lamarckiana*, Oesterr. bot. Zeitschrift, 1895, Nos. 5-6.

the artificial fertilization of the whole ancestry in my pedigree-cultures.

Fig. 46. *Oenothera lata.* Top of a stem, with buds in the axils of the broad bracts; *a, b, c,* separate buds in various stages of development; A, B, C, buds of *Oenothera Lamarckiana* in corresponding stages. The buds of *lata* are seen to be palpably fatter than those of *O. Lamarckiana.*

O. lata can easily be distinguished at every stage of its existence from all its allies; in fact as soon as the

second or third leaf unfolds: these leaves are broad with broad bases and long petioles. But most characteristic is the broad and round shape of the tip of the leaf, a feature which is more or less distinctly pronounced during all the rest of the life of the plant. The plants are always low although the rosettes are large and strong, stronger sometimes than those of *Lamarckiana* itself. The stem is limp so that the top hangs over to the side even in the healthiest plants. It is thickly covered with dense foliage. The leaves are rounded at the apex and much crumpled. The top of the growing stem, both in its young stages and when it is covered with flowers, is in the form of a compressed rosette.

Everything in this plant is stout and broad, so that they came to be known among us in the garden as "fatheads." This character was particularly noticeable in the case of the flower-buds just before they opened, and has been well brought out by POHL's figures. The petals do not unfold themselves completely but remain more or less wrinkled. The stigmas are peculiar. As in the case of *O. Lamarckiana* their number varies from a normal of four up to 8 and more, forming a so-called half-curve. This matter has been made the subject of a thorough study by VERSCHAFFELT in the case of *O. Lamarckiana.* The fusion of neighboring stigmas. which occurs in the parent form, occurs in *O. lata* also. The unequal development of the stigmas which occurs now and again in *Lamarckiana* is exaggerated to an extraordinary extent in the daughter species; and the most curious malformations arise as the result of the fusion referred to.[1] They do not however interfere with fertilization.

[1] For figures of these see POHL's paper, *loc. cit.*, Taf. X, Fig. 27.

The fruits are short and thick and contain relatively few but, as a rule, large seeds.

O. lata appeared pretty regularly in my cultures, but in proportions which varied greatly. And as they could be easily and certainly recognized, even under unfavorable circumstances such as crowding, these deviations are indices of a real variability in proportions and not of the difficulty of identification which may have affected the proportions in the case of the other forms. The proportion of *lata* plants was sometimes as low as 0.1%; in the fifth generation it was as high as 1.8%; i. e., about the same as that of *O. oblonga.*

VII. *O. scintillans.* Except for *O. gigas* which has so far only arisen three times, and *O. spathulata, O. subovata, O. leptocarpa* and others which I shall refer to later on, *O. scintillans* is by far the rarest form in my cultures. It arose only eight times in the *Lamarckiana*-family, and in other families still more seldom.

It does not, like the other species, breed true when self-fertilized, but behaves in a very peculiar way. Seeds from it give rise to three forms in considerable numbers: *O. scintillans, O. oblonga* (Fig. 44 on page 233) and *O. Lamarckiana.*

This is a different phenomenon from that with which we are already familiar in the other elementary species, namely the very occasional production of a mutation in about 1 in 1000 plants. There often arise in this way elementary species of the second order, i. e., species which combine the characters of two species. These also arise in the case of *O. scintillans*; e. g., *O. scintillans nanella* and *O. scintillans elliptica.* But only very occasionally, i. e., one such among thousands of normal *O. scintillans.*

A very remarkable feature of this instability of *O.*

scintillans is that the proportions, in which the different forms occur, are by no means low at first, and that they cannot be increased by selection. Perfectly definite principles underlie these proportions; for the behavior of an *O. scintillans* from one stock is the same as that derived from another.

Fig. 47. *Oenothera scintillans.* Top of an annual plant.

Some mutants of *O. scintillans* had a capacity of producing 35-40 % *scintillans*; and others a capacity of producing 70 % or more. Moreover, this capacity seems to be inherited.

I first noticed *O. scintillans* in 1888, in a culture from seeds of the *lata*-family (§ 7). The plant was biennial: I did not sow its seeds till 1894. In 1895 I fertilized some of them (which, it will be seen, flowered in their second year) with their own pollen. I treated 14 plants in this way, but they set little seed. In 1896 I raised only 400 plants from them as follows:

68 % *O. Lamarckiana*
15 % *O. scintillans*
15 % *O. oblonga*
2 % *O. lata*

and one plant of *O. nanella.*

In 1898 there arose in another *O. lata*-family a single example of *O. scintillans* which flowered in its first year and was self-fertilized in a bag. 148 young plants were raised from its seeds, as follows:

55 % *O. Lamarckiana*
37 % *O. scintillans*
7 % *O. oblonga*
1 % *O. lata.*

I have tested the hereditary capacity of three examples of *O. scintillans* which arose directly from the *O. Lamarckiana*-family. The first was a plant which arose in 1895 but did not flower till 1896; it had a number of lateral stems on all of which the flowers were fertilized. The various sowings of their seeds gave the following species and proportions:

52-59 % *O. Lamarckiana*
34-36 % *O. scintillans*
3-10 % *O. oblonga*
1 % *O. lata.*

I managed to obtain self-fertilized seeds from numerous *O. scintillans* which appeared in this culture; the proportions of the various kinds produced by them were subject to considerable fluctuation, but they were essentially the same as those given by their parents.

Of the six plants which, as shown in the table on page 224, arose (1896) in the fifth generation of *O. Lamarckiana* I only succeeded in bringing two through the winter and in getting them to flower (1897). They were self-fertilized in bags. The seeds of one plant gave like the others:

51 % *O. Lamarckiana*
39 % *O. scintillans*
8 % *O. oblonga*

1 % *O. lata*
1 % *O. nanella.*

But the second plant gave a much "better" result for the 200 seedlings were distributed as follows:

8 % *O. Lamarckiana*
69 % *O. scintillans*
21 % *O. oblonga*
2 % *O. lata, O. nanella,* etc.

I fertilized about 25 of those *O. scintillans* with their own pollen. I sowed the seeds of each one separately and got a proportion of *scintillans* in the next generation varying between 66 and 93 % about a mean of 84 %. One plant seemed to give *O. scintillans* only; but the crop from this plant was small. In 1899 and 1900 I continued my experiments in the same way, in order to find out whether this species could be brought, by selection, to the same level of constancy as that which characterizes the other elementary species.

Perhaps some day there will appear in the *Lamarckiana*-family or in some other a *scintillans* which will breed true straight away.

An estimation of the constancy of *scintillans* mutants has been made four times in all. Three times it gave offspring like itself in the proportion of 34-39 %; in the next generation it did the same. In the fourth instance the proportion was 69 % and the mean, in the next generation, had mounted to 84 %. These numbers show in my opinion that *O. scintillans* is an inconstant species which moreover tends to give rise on its first appearance to other forms and especially to *O. oblonga.*[1]

[1] The deviation in the first series of figures (15 % instead of 34-39 %) which occurred in a second generation, from a *scintillans*

It now remains to give a short description of the specific character of this form.

Scintillans cannot be recognized until quite late:[1] as a rule they could not be identified before the rosettes had quite a considerable number of leaves about 10 cm. long. The leaves are small, narrow and with long petioles; with shiny surface (whence the name), dark green, and with hardly any trace of crumpling. The veins are white and often broad. The ends of the leaves turn down, so that the leaf makes an arch over the ground. The stems never attain a great size; they are thin and bear short leaves; they produce flowers early, forming long spikes. The annual forms are usually only feebly branched; the biennial ones more profusely. The flowers are small; a little smaller or about the same size as those of *O. biennis*. As in *O. Lamarckiana*, the stigmas project beyond the anthers. The fruits are small, the quantity of seed in annual plants is also small; and many of the plants begin to flower too late to set any seed at all.

The dark green color and shiny surface occurs on the stem leaves as well, and gives the plant a peculiar appearance quite different from that of *O. Lamarckiana*.

§ 4. THE LAWS OF MUTATION.

I propose now to recapitulate the conclusions which I have drawn from my experiments. The various elementary species we have dealt with behave in essentially the same way; so also does a secondary branch of the

whose proportion in the first generation is unfortunately unknown, seems also to point to some susceptibility of this proportion to factors we do not yet understand.

[1] Since writing this, I have succeeded in recognizing them as young seedlings, with only 2-4 leaves (Note of 1908).

family we have just considered, as well as two other primary families which will be described in section 5; not to mention a number of subsidiary families and cultures. The main conclusion is that the facts of mutability can be described by laws just as definite as the laws of variability.

The following generalizations apply in the first instance to the new forms which have arisen from *Oenothera Lamarckiana*; but it should be stated that they are completely in accordance with a whole host of observations, for the most part of a horticultural nature, on other genera and families.

I. *New elementary species arise suddenly, without transitional forms.* A great point in my experiments has been that the ancestors of the newly arisen forms have always been accurately known, and often for many generations back; and that they were either isolated as a group (1887-1891) or that they flowered in isolating-bags and were artificially fertilized (1894-1899). There is no mention of any such precaution in horticultural records. This precaution enables us to be certain that each new form arose from the seed of a normal specimen of *Oenothera Lamarckiana*. The new form always arises with all the characters proper to it. Once the identity of a seedling is recognized the characters which it will gradually assume can be predicted, and in every case the prediction has been fulfilled.

Many opportunities for testing the degree of certainty in identifying seedlings offered themselves during the course of the experiments, and especially when the chosen seedlings were planted out and flowered in my garden.

When there are hundreds of individuals to record,

it is natural that one should occasionally be in doubt over some of them; particularly over such as happen to grow between others, and have not, on that account, sufficient space for their full development. I have usually given these plants an additional lease of life, in many cases the whole summer. They then very soon proved to be a pure type; or perhaps, to be compound forms such as *O. lata nanella, O. scintillans elliptica* and so forth, or, lastly, new forms altogether. But they never turned out to be intermediate forms. Transitions between the various elementary species did not occur.

As a matter of fact I have thought on one or two occasions that I had discovered examples of such intermediates. For example I once noticed a plant which was like *O. lata* in many respects but bore plenty of pollen. I fertilized the plant artificially and raised 270 plants from its seed. These were all like their parent except for 1 % of them which were true *lata,* that is to say no larger a percentage of *O. lata* than the *Lamarckiana*-family itself can give rise to. I have called this form *O. semilata* (§ 17). Other cases of a similar nature have been observed.

The seed of a newly arisen form will, if sown, always give rise to plants with exactly the same characters as their parents; and this purity of the new form is maintained in subsequent generations.

II. *New elementary species are, as a rule, absolutely constant from the moment that they arise.* The seeds set by an example of a newly arisen species after artificial self-fertilization give rise solely to plants like itself; without, as a rule, any trace of reversion to its parental form.

This is equally true of *O. gigas* which has only arisen

three times, and of forms which have appeared as frequently as have *O. albida, O. oblonga, O. rubrinervis* and *O. nanella.*

The point cannot be decided in the case of *O. laevifolia* or *O. brevistylis,* both of which were found on the spot where *O. Lamarckiana* was originally discovered, but have not arisen in my cultures. Both these, when self-fertilized, come perfectly true from seed. *O. brevistylis* breeds true in spite of its small fruits which sometimes set no more than a solitary seed. Indeed I thought at first that these fruits were absolutely sterile.

Oenothera scintillans and *O. lata* are exceptions to this rule. The seeds borne by self-fertilized plants of the first named form produce a generation only about one-third of which is *O. scintillans.* This is true of the seeds of three distinct individuals which have arisen quite independently of one another. From the seed of a fourth individual however 69 % of *O. scintillans* were raised; and these again in the next generation gave from 60 to 90 %.[1]

This constancy of the new species is an extremely important characteristic. It has enabled *O. laevifolia* and *O. brevistylis* to maintain themselves in the spot where they arose—mere scattered examples among the host of *Lamarckianas* which surround them; and, what is more, pure in respect of all their characters (apart of course from accidental crossing)

That the struggle for existence is a pretty keen one in the field in question may be gathered from the fact that a vigorous *Lamarckiana* can bear 100 fruits and that each fruit contains between 200 and 300 seeds. The whole

[1] For further information on this point see section 19 of this part.

field contains no more than some thousands of plants, that is to say not much more than could be supplied by the seeds of a single individual. The seeds which do not produce adult plants either do not germinate or the seedlings which come up die young. Yet in spite of the severity of the competition, *O. laevifolia* and *O. brevistylis* have maintained themselves for more than twelve years.[1]

III. *Most of the new forms that have appeared are elementary species, and not varieties in the strict sense of the term.* Elementary species are distinguished from their nearest allies by nearly if not quite all their characters. The differences are often so slight as to escape notice by an eye not trained to observe them; and they are particularly apt, as systematists so often complain, to become lost in dried specimens. This latter is however fortunately not the case with the new forms whose origin I have witnessed; for they are distinguishable from one another and from *O. Lamarckiana* as herbarium specimens far more easily than, for example, specimens of this last species are from *O. biennis*.

This close familiarity with each form can only be attained by a careful and minute study and description of all the organs of the plant at every stage of its development. Once a plant is thoroughly known in this way it can be recognized at almost any stage.

Varieties are distinguished from the mother species usually by one single character or at most by two or three, whilst they resemble them in all others. Apart from this point, the difference between species and varieties is to a large extent arbitrary, since when tested experimentally the one is just as constant as the other.

[1] And afterwards until now (Note of 1908).

It is rather curious that all the new forms which have arisen in my experiments should have been species in this sense and not varieties. I have always hoped to get a white flowered form or some other such distinct variety but so far in vain. *O. nanella* is perhaps the only form which can be called a variety in the horticultural sense of the term.

It is a charcteristic of varieties that they crop up in a great number of unrelated species, genera and families. For example the varieties *rosea, alba, laevis, inermis, laciniata, prolifera, bracteata,* and *pendula.* It is the same with monstrosities: e. g., var: *plena, fasciata, torsa, adnata, fissa* and so forth. The same is true of dwarfs or the var. *nana.*

But with the exception of *O. nanella* I cannot find in other families and genera any series of forms analogous to mine. It is for these reasons that I do not consider them varieties.

A very popular definition of varieties is that they are forms which are known to have arisen from other forms. This position is obviously untenable. The proof of their origin may exist in the case of some few horticultural varieties but with the vast majority of them and with all wild varieties this proof does not exist at all. Their origin is a thing of the past and when, as is usually the case, it was not witnessed by human eyes the so-called "proof" of it is based on deduction or analogy.

And in all cases, where we are not dealing with direct observation, the origin of varieties is in no sense whatever more certain that that of collective species or genera.

I have dwelt on this point because I feel quite certain that many of my readers will regard my new forms as

varieties *for the very reason that I have been able to observe their origin.*[1]

IV. *New elementary species appear in large numbers at the same time or at any rate during the same period.* SCOTT's palæontological results have led him to conclude that species-forming variability, or, as he also calls it, mutability must appear simultaneously in large groups of individuals and that the causes of these changes have probably been working through long periods of time.[2]

The palæontologist investigates the problem of the origin of species only in broad outline. It is the experimental physiologist who deals with the separate individuals themselves and with their posterity, of whom not a millionth part would ever be preserved in the fossil state. We have no right therefore to expect more than a general agreement between the conclusions attained by these two lines of investigation.

And when we do find such agreement, as we do in the present instance, I think it is extremely desirable that it should be put on record.

Amongst the species which have arisen in my experimental garden *Oenothera gigas* has only been observed once. The others appeared every, or nearly every, year in varying, and often, indeed, in considerable numbers. More than 800 individuals of the seven new species we have described arose independently from one another from the *Lamarckiana*-family. And as about 50,000 plants were cultivated during this period of time the

[1] Fortunately, as a matter of fact, this has not been the case (Note of 1908).

[2] W. B. SCOTT, *On Variations and Mutations*, Amer. Journ. Sci., 3d Ser., Vol. 48, No. 287, Nov. 1894. See p. 373. "Forces both external and internal similarly affect large numbers of individuals."

number of new forms amounted to between 1 and 2 % of the total cultivated.

In other words: *The new elementary species arose from the parent form in a ratio of* 1-2 %. *Sometimes more than, but oftener less than, this value.* And this ratio was maintained throughout the whole course of my experiment, so far, at least, as the difference in the methods of investigation which have been employed at different times permit me to estimate it.

This figure, 1-2 %, is more probably too small than too large. For it was only in the years 1895 and 1896 that I went to the labor of determining it accurately. In previous years the average was considerably lowered by other circumstances, the most important of which was the omission of such forms as *O. oblonga, O. rubrinervis* and *O. scintillans* which at that time I could not recognize in their early stages. The table on page 224 shows, for the two years 1895 and 1896, 22,000 individuals of *Lamarckiana* and 711 of the new forms. *That is, more than* 3 %.

O. laevifolia and *O. brevistylis* formed far smaller a percentage than 3 % of the number of *Oenotheras* growing on the original field at Hilversum; yet they, obviously, arose in quantities sufficient for them to maintain themselves. We may conclude therefore that a yearly appearance in the proportion of from 1 to 3 % would be sufficient for the establishment of a new species.[1]

V. *The new characters have nothing to do with individual variability. Oenothera Lamarckiana* exhibits a degree of fluctuating variability in all its characters which is certainly not less than that exhibited by other plants. The new species fall right outside the range of

[1] Compare the calculations of DELBOEUF, as given above (I § 28).

this variability; as is evident from the fact that they are not connected with the parent type by intermediate or transitional forms.

New races can of course be evolved by repeated selection in one or another direction in *Lamarckiana* just as much as in any other plant. Indeed I have, myself, produced a long-fruited and a short-fruited form in this way. But such races remain dependent on selection and differ from their type only in one feature: they do not bear the slightest resemblance to elementary species.

Elementary species themselves exhibit fluctuating variability, and often indeed to a greater extent than the parent form. Nearly all their organs and characters vary, but never in such a way as to approach the original form.

VI. *The mutations, to which the origin of new elementary species is due, appear to be indefinite, that is to say, the changes may affect all organs and seem to take place in almost every conceivable direction.* The plants become stronger (*gigas*) or weaker (*albida*). with broader or with smaller leaves. The flowers become larger (*gigas*) and darker yellow (*rubrinervis*), or smaller (*oblonga* and *scintillans*) and paler (*albida*). The fruits become longer (*rubrinervis*) or shorter (*gigas, albida, lata*). The epidermis becomes more uneven (*albida*) or smoother (*laevifolia*); the crumples on the leaves either increase (*lata*) or diminish (*scintillans*). The production of pollen is either increased (*rubrinervis*) or diminished (*scintillans*); the seeds become larger (*gigas*) or smaller (*scintillans*), more plentiful (*rubrinervis*) or more scanty (*lata*). The plant becomes female (*lata*) or almost entirely male (*brevistylis*); many forms which are not described here were almost entirely sterile, some almost destitute of flowers.

O. gigas, O. scintillans, O. oblonga tend to become biennial more than *O. Lamarckiana*; and *O. lata* tends to become less so; whilst *O. nanella* cultivated in the usual way scarcely ever runs into a second year.

This list could easily be extended, but for the present it may suffice.

To regard the new forms from another point of view, some of them are fitter, some unfitter than the parent form, and others neither the one nor the other. Until experiments have been made with the new forms sown in the field it is obvious that no definite conclusion on this point can be arrived at: nor do the observations which have so far been made on the plants growing in the field at Hilversum throw any light on the subject.

Nevertheless it is evident that the female *O. lata* is at a great disadvantage; and that *O. albida* with its narrow leaves is, at any rate in its early stages, far too delicate. *O. rubrinervis* looks quite robust but is very brittle and liable to be broken. Annual plants of *O. oblonga* bear hardly any seeds, whilst *O. nanella* is very small and its petioles are often brittle. All these forms appear to me to be less fit as compared with *O. Lamarckiana.*

On the other hand *O. laevifolia* seems to be at least a match for its parent; and *O. gigas* in many respects superior to it: all its organs are larger and stronger and apparently better adapted to perform their functions; the whole plant is stouter. Sowings of this species in the open should give favorable results.

The forms which have not yet been described (*O. spathulata, subovata,* etc.) are hampered in the struggle for existence by their almost complete sterility. *O. sublinearis* with its slender grass-like leaves is much too weak in its early stages—and so forth.

Many authors already hold that species-forming variability must be indiscriminate. We are strongly opposed to the conception of a definite "tendency to vary" which would bring about useful changes, or at least favor their appearance. The great service which DARWIN did was that he demonstrated the possibility of accounting for the evolution of the whole animal and vegetable kingdom without invoking the aid of supernatural agencies. According to him species-forming variability exists without any reference to the fitness of the forms to which it gives rise. It simply provides material for natural selection to operate on. And whether this selection takes place between individuals, as DARWIN and WALLACE thought, or whether it decides between the existence of whole species, as I think; it is the possibility of existence under given external conditions which determines whether a new form shall survive or not.

We can go a step further and say that many more useless and unfavorable variations must arise than favorable ones. This becomes sufficiently evident when we consider the complexity of the conditions which an organism has to satisfy before it can supplant its fellows.

The mutability of *Oenothera Lamarckiana* satisfies all these theoretical conditions perfectly. Nearly all organs and all characters mutate, and in almost every conceivable direction and combination. Many combinations must obviously be fatal to the life of the germ within the ripening seed and cannot on that account be observed. Others hinder the development of the seedlings and whole series of experiments with apparently mutated plants came to nothing in spite of every care on account of the premature death of the young plants. Many combinations reduce the fertility so much that we cannot go fur-

ther than observe the mutated individual itself. A number of other combinations are, I suppose, lost in my experiments because they cannot be detected until the plants are fairly old, by which time the great majority have been weeded out to make more room.[1] Such considerations seem to me to explain how it was that I was able to cultivate only so small a number of new species through more than one generation. And it is of course open to question how many of those that I did cultivate could survive the struggle for existence.

I conclude therefore: Mutability is indiscriminate. Some mutations bear no offspring and disappear forthwith. Between the others and the species already established natural selection must decide, unless artificial selection steps in.

VII. *Mutability appears periodically.* I am led to this conclusion by my experiments; but I express it at present only tentatively. The fact that of all the species that I have examined so far, only one has proved to be in a state of mutation appears to me sufficient evidence for this conclusion. But further investigations are necessary for the establishment of the generalization: and such I have only recently started. I am not of course now in a position to give experimental proof of the existence of mutable and immutable periods: but I have enunciated the hypothesis of their existence as the simplest explanation of the remarkable fact that I have so far observed mutations only in a single species; though plentifully enough in it.

The above generalizations refer in the first instance to the case which we have observed, namely the muta-

[1] For example *O. brevistylis* and *O. leptocarpa* are not recognizable until just before they flower.

bility of *Oenothera Lamarckiana*. But inasmuch as experimental investigation of other instances has not yet been published, we must, pending the acquisition of that knowledge, regard it as a typical case of the origin of new species.

§ 5. A BRANCH OF THE LAMARCKIANA-FAMILY.

In 1895 I started a culture which may be regarded as a branch of the main line of descent which has already been described. My object was to try to get more mutations by increasing the sowings. I used the seed which had been harvested in 1889, a part of which had already been employed in the culture summarized on p. 224. The available quantity of seed amounted to about 230 ccm. and was all sown.

In November 1888 I picked out from among the plants that I had saved during the summer the 12 strongest; and planted them on a separate bed where the conditions were very favorable owing to the fact that the position was a sunny one, and that it was far away from any other *Oenothera* cultures. In the spring of 1889 I reduced the number to 6, which grew up to fine well-branched plants. Each plant flowered not only on its main stem and its branches but also on the numerous branches which sprang from the axils of the radical leaves. Superfluous lateral branches were however cut away in July. Each plant furnished from 25-50 ccm. of seed and the seed from separate plants was harvested separately. The pollination of the flowers, which were not enclosed, was left to insects. I sowed the seed as evenly as possible on a bed of 12 square meters, keeping the seed of the 6 seed-parents in separate lots. As soon

as the young seedlings were identifiable they were recorded and removed. Those which bore the characters of their parents were simply pulled up and thrown away with the exception of some which did not interfere with the growth of their neighbors and could therefore be allowed to flower. The mutants were always carefully removed and planted singly in pots with rich garden-soil for further experiment. This sorting lasted from the middle of May till the middle of June.

The *lata* and *nanella* plants were recognizable at a very young stage and so could be transplanted in large numbers before they became overshadowed and overgrown by the plants which surrounded them.

The same was true of *albida* which was however always very delicate. Not until a much later stage of growth was *oblonga* recognizable; and later still *rubrinervis*. At this time the bed was thickly covered with the rosettes, the stronger ones overgrowing the weaker ones. There can be hardly any doubt that many mutants especially of the *rubrinervis* and the other rare types perished in this way before I was able to recognize and transplant them. Therefore the figures given underestimate rather than overestimate the actual number of mutants.

About the middle of June the plants were so crowded that there was no longer any hope that any particularly late mutant could maintain itself. I then simply thinned them out as much as was necessary to give those that remained room to flower. In August about 700 plants flowered. Later on two of these attracted attention by the great length of their stems which were much longer than those of the rest and towered above them. They turned out to be a new form which has appeared again in other strains and will be termed *O. leptocarpa*. Apart

from these the beds contained nothing but pure *O. Lamarckiana*: I examined them repeatedly and thoroughly during the whole time that they were in flower.

I harvested the seed in October and took care that as few as possible fell to the ground; for it still contained a good deal of seed from the original sowing which I expected to germinate in the following spring.

I had already become acquainted with this belated germination in one particular case. In March 1887 I sowed some thousands of seeds; they germinated during the course of the whole summer and at the end of each month the seedlings were counted and pulled up. Up to the middle of April 908 germinated; between then and the middle of May 288. From the 14th of May to the 14th of July only 64 germinated: from then till the 14th of September 130; and between that date and the middle of October only 6. During the winter there was no germination although the sowing-pans were protected from the frost and the circumstances were favorable in every other way. Up till the middle of March 1888 there appeared only three seedlings. But then—in the *second* spring — an extraordinarily large number appeared.[1] Within 14 days 272 plants had unfolded their leaves, and others followed as before in gradually decreasing numbers. The latest seeds stayed for 2 or more years in the ground before they germinated.

In the spring of 1896 therefore I expected the seeds which had remained in the ground from the previous spring to germinate. Whilst this was taking place I counted the mutants and transplanted them singly into pots as before; I weeded out the normal individuals as

[1] A similar phenomenon is known to occur in the case of species of clover, *Primula* and many other plants.

early and as completely as possible, without counting them. I found, altogether, 102 mutants but in quite different proportions to that in which they appeared in the previous year. Particularly was this the case with *albida* and *lata* which were very rare and with *rubrinervis* which was relatively plentiful.

I shall now display the result of this experiment in the form of a genealogical table similar to that on page 224. The two parts of the last generation which appeared in the two successive years are entered separately.

OENOTHERA LAMARCKIANA.

A

THE LAMARCKIANA-FAMILY.

II

TABLE TO SHOW THE ORIGIN OF NEW SPECIES IN A BRANCH OF THE MAIN CULTURE.

(The figures refer to the numbers of individuals.)

GENERATIONS		SPECIES								
		albida	oblonga	rubrinervis	O. Lam.	nanella	lata	scintillans	ellipticа	leptocarpa
III B	3rd gen. second year 1896	1	54	8	—	35	3	0	1	0
III A	first year 1895	255	69	1	10,000	111	168	1	7	2
II	2nd gen. (biennial) 1888–1889				6					
I	1st gen. (biennial) 1886–1887				9					

The whole number of mutants in the year 1895 amounted therefore to 614 or about 6 %, of which *O. albida* made up 2.5 %, *O. lata* 1.7 %, *O. nanella* 1.1 %, *O. oblonga* 0.7 % and the rest altogether 0.1 %. I have not calculated the percentages of mutants for the year 1896, in which 102 occurred.

The figures show a very good agreement with those which will be found in the table on page 224. There are of course divergences of detail, as is only to be expected. But similar divergences were also found between the numbers produced by the 6 different plants. I have not thought it worth while to give these here in detail; suffice it to say that the commoner mutants occurred in each of the six sowings though in varying proportions.

One of these six sowings gave a highly unexpected and interesting result. It was the most extensive one; 75 ccm. of seed was sown on 4 square meters of soil; that is to say as much per square meter as for the 5 other plots. These seeds did not do at all well. In 1895 only 350 germinated that is 5 per cubic centimeter, whereas usually 70 per cubic centimeter germinated.[1] These 350 seeds gave rise to the number of mutants shown in column A.

Number of mutants per 4 square meters.

	A	B
O. albida	64	95
O. oblonga	9	30
O. rubrinervis ..	1	0
O. nanella	0	55
O. lata	61	54
Totals	135	234

[1] A cubic centimeter contains about 500 seeds.

For comparison I give in column B the mutants produced by the five other mothers per similar area under cultivation or per 4 square meters.

If we reckon the percentage of mutants among the seedlings derived from this particular mother we find it to be about 40 % instead of the 6 % of the whole culture (or the 5 % of the 5 other mother plants).

But if we calculate this figure *per cubic centimeter of seeds* we find it to be for this plant 1.8, but for the rest 3.2.

The absolute total of mutants is therefore reduced to one-half through failure to germinate, whilst the absolute number of seeds that germinated was reduced from 70 to 5 per cubic centimeter. The percentage of mutants from the seeds which did germinate rose, therefore, from 5 to 40 %.

The failure to germinate was in all probability due to the fact that the seed had been kept for 5 years; but it is difficult to see why this should have affected one sample of seed and not the five others. When seeds are kept they gradually die off, some sooner, some later.

It follows from the facts described above that mutating seeds do not die off so soon as, or remain capable of germinating longer than normal *Lamarckiana* seeds. It is only the seeds of the dwarf form that appear weaker than the parent species and perhaps also those of *O. elliptica*.

Should this phenomenon prove to be a general one it should be possible by artificially hastening the death of the seeds to materially increase the percentage of mutants in a given sample. Such a discovery would immensely facilitate the search for mutations in the vegetable kingdom.

I must now return to the transplanted seedlings. Several of them were weak, and died sooner or later; especially the most easily recognizable of them all, *O. albida.* In the case of others too many were raised for them all to flower. But I grew the majority of them during the whole summer; some of them flowered; others remained in the rosette stage. I saved seeds from *O. albida* in 1897 (from plants which came up in 1896) from *O. rubrinervis, O. nanella* and *O. scintillans.* The first three when self-fertilized bred true, the last did not (see page 244). Further details on this point will be given in the second chapter under the heading of the plant in question.

§ 6. THE LAEVIFOLIA-FAMILY.

In 1887, I noticed in the locality for *Oenothera Lamarckiana* near Hilversum, a group of individuals whose peculiar characters showed them to be a distinct form. I therefore gathered some of their seeds and sowed them in the following year in my experimental garden. They gave rise to two forms (as was to be expected from the fact that no attempt was made, or was possible, to insure self-fertilization) of which the one was the ordinary *Lamarckiana* whilst the others were like the parent plant. I propose to call this subspecies *O. laevifolia* on account of its smooth leaves which are not or at any rate scarcely perceptibly crumpled, as is the case in *Lamarckiana.*

For the first few years I let the two forms grow and flower together and took no further precaution than isolating them from the rest of the cultures. In the year 1894 I began the practice of enclosing the blossoms before opening in paraffined paper bags and of fertilizing

them with their own pollen. They have since that time bred true and given rise to no more *O. Lamarckiana*; nor have they, since that time given rise to any mutations.

How and when *O. laevifolia* arose I do not of course know. It was already there when I visited the locality for the first time. But it grew there in a special isolated spot in such a way as to make it probable that the plants had grown from the seeds of a single parent which we must suppose had arisen there not so very long before.

I propose, therefore, to give a somewhat detailed description of the original locality. I shall have frequent occasion, when I shall be describing other families or individual species, of referring to it again.

On the estate of Jagtlust, the property of Dr. juris J. Six, between Hilversum and 's Graveland in the Netherland province of North Holland there was at one time a potato field, whose southern boundary bordered on a canal which had been dug many years before. About the year 1870 the owner had a new branch of this canal dug which followed the western boundary of the field, and completely shut off any access to it from the north. So that the field became accessible only from the east where there was no road; and it consequently became impossible to let it. From that time it lay fallow; and in the first few years was not dug any more than was necessary for the laying of a few paths and the planting of a few trees. It obviously afforded wild plants a splendid opportunity of almost unlimited multiplication. *Oenothera* had seized this opportunity somewhat later than the other wild plants in the neighborhood and although it did not spread as fast as they, it took fuller advantage of the field in the end.

Near the field, there was a small bed in a park in which some annuals were grown every year. Amongst these was *Oenothera Lamarckiana* which spread from this spot over the field. When I first visited the place the little bed had long since run wild, but was still recognizable. The *Oenotheras* were most numerous on the northeast corner of the field, close to the bed they spread from. Here they formed a dense jungle of branched stems as high as a man. The area of the whole field was about 5000 square meters.

This dense group was surrounded by a broad zone of plants a few of which were in flower, and of numerous rosettes, growing together; whilst to the west of this zone only isolated rosettes were to be found. But on the greater part of the field not a single *Oenothera* was to be seen at first glance; though, after further search I found flowering plants in two places, and in five or six other places rosettes with radical leaves, evidently from seed which had germinated that spring.

We may conclude therefore that the plants began to spread from the northeast corner of the field in the period 1884 to 1886. In 1888 the whole field had become occupied by isolated groups consisting of both young and two-year-old flowering individuals.

In the winter 1886-7 and 1887-8 a part of the northeast corner of the field comprising more than one-half of the *Oenothera* patch was deeply dug and planted with oaks. But the ground was so full of seed that for two summers afterwards, this piece was thickly covered with rosettes and flowering plants of *Oenothera*. One result of this was a very high degree of variability in the duration of life of the plants, for there could be seen on this spot during the month of August and September numer-

ous stems of every conceivable height between rosettes which had not yet developed a stem and tall flowering plants.

In 1889 the owner of the property, having decided to plant the rest of the field with trees,[1] had two straight paths made, intersecting each other, and a semicircular path to round off that side of the field which did not abut on the canals. On both sides of these paths the ground, which is almost pure sand, was dug up to a depth of three or four feet and planted with young trees. Many *Oenotheras* were of course destroyed in this way, but since that time they have spread more rapidly than ever. The newly turned soil seemed to suit them; for they grew on it in the most extraordinary profusion and extended from it in all directions over the whole field whose easterly half they had almost completely covered by 1894.

It is more than natural that from such a center the plant should have gradually spread in the neighborhood. As early as 1888 I found it in one or two fields a good way off, and since then it has occurred elsewhere; but always in relatively small numbers.

As soon as I had become acquainted (1886) with the spot in question on the deserted potato field I saw that here was a wonderful opportunity of getting some insight into the phenomena of variation as exhibited by a plant which was multiplying rapidly. The diversity in the form of the leaves, the height of the stem and the mode of branching etc. exhibited a very high degree of variability, and when the large bright yellow flowers opened in July and August I saw that almost every single

[1] In consequence of this the field is now entirely covered with wood, partly consisting of oak and partly of pines, leaving hardly any room for *Oenotheras* to grow. (Note of 1908.)

character was highly variable. A whole series of variations in the flowers not hitherto described for this species, was found in the first few days and many more of them were noticed when I visited them later.

In 1886, 1887 and 1888 I spent the whole summer at a spot a few minutes walk from the field and so had the opportunity of studying this single species for hours at a time every week and often, even, every day. Since then I have visited the place nearly every year, often indeed twice or oftener, every year; or I have had accounts of it from others; so that I have been able to follow the progress of events step by step by collecting accounts of the behavior of old mutations, and of the origin of new ones on the field.

But it soon became evident that to follow the sequence of events more closely the investigation must be continued on the lines of experimental culture. Mr. Six kindly agreed to my taking some first year rosettes and seed from the field. My object in doing this was twofold. In the first place (we will suppose for the moment that we are justified in regarding the deviations exhibited by an individual as already present in the seed which produces it) we learn by sowing in the garden the seed gathered in the field, in a far more certain and precise manner, what new forms would be produced in the field. In the second place I have saved seed from the plants thus raised in the garden and have sown them and have in this way raised the different "Families" each of which has its origin on the field at Hilversum, and has, in great part, repeated the process of mutation under daily control in my experimental garden. It is evident that in this way a much more accurate investigation of heredity was made possible than could ever have been

carried out in the field. Of such families I possess three, as I have already stated. The *Lamarckiana*-family arose from rosettes, the *lata*-family from seeds gathered in 1886, and the *laevifolia*-family, with which this section deals, from the small group of that species that was found in the field (1887). The hereditary phenomena which they exhibited afforded a clearer insight into these processes than could be derived from the observations in the original locality.

I propose to offer now some remarks on the incompleteness of field-observations and on some difficulties of experimenting in a garden. If every mutation was a favorable one and gave rise to individuals which had a good chance of surviving in the struggle with their neighbors in the field, and with unfavorable climatic conditions in the cultivated state, many a new form would have come under observation, which, as it is, must have perished in its youth. But most new species are weaker than their parent, for example by having smaller leaves, and therefore grow more slowly; some are partly or absolutely sterile in one sex and therefore cannot be perpetuated at all except by crossing; whilst others come to nought for unknown reasons.

Variability in the duration of life is especially unfavorable; and may become positively dangerous in cultivation. Normal annual and biennial individuals can be easily made to flower and to set seed, although inability to resist cold has been the cause of the loss of some of my most interesting rosettes. On the other hand there often occur plants which behave as if they were going to be annual but grow their stem too late to set seed or even, in many cases, to flower at all, before they are carried off by the winter. In the case of several of

my new species it was not until many years had elapsed that I succeeded in getting them to flower and ripen their fruits—as for example *O. albida* and *O. elliptica.*

I must now return to *O. laevifolia.* I found it first in 1887 when I came across ten specimens which could be recognized as a new type by the oval, as opposed to heart-shaped, petals of the flowers of their lateral branches.

Five of these plants formed the nucleus of a little group of about a hundred individuals which stood in the northwest part of the field far removed from any other *Oenotheras.* In the previous year I had seen on this spot some first year's rosettes, but no flowering plants. At greater and lesser distances from this center there grew five other plants in rather isolated positions in the field which was still poor in *Oenotheras* in this region.

In the following year I found this type in the same spot but not elsewhere.

Since that time *O. laevifolia* has maintained itself on the field in such a way that the original spot, which was easily recognizable by certain features, has continued to form the nucleus of the whole group. In subsequent years I have found the species in other parts of the field also—but as rare and isolated examples only. The numbers of it, however, on the original spot have gradually if slowly increased; the group consists, doubtless as the result of mixed fertilization by insects, partly of *O. laevifolia* and partly of *O. Lamarckiana.* Since 1894 that part of the field has been completely overgrown with *Oenotheras* so that the limits of the original group have disappeared.

This mode of distribution of our plant round a definite center for a period of eight years coupled with the

fact that it was allowed to cross freely with the parent species clearly indicate the operation of some definite hereditary process. Whether the ten plants of the first year (1887) had a common origin cannot of course be decided *a posteriori,* but it cannot be regarded as other than extremely probable.

I now come to the cultures in my experimental garden. For these I collected, as I have already said, the seeds of some examples of *O. laevifolia* in the field at Hilversum towards the end of the summer of 1887.

These seeds produced in my garden in 1888 over 200 plants of which about 60 % were annual; some of them were *O. Lamarckiana* and some *O. laevifolia.* I selected the seed from the strongest and most precocious examples of the crop for the cultivation of the family, keeping, of course, the two species separate.

In 1889 three beds of 10 square meters were sown with the seeds of the *O. Lamarckiana* plants partly in the hope of getting new forms and partly with a view to an investigation, to be described later on, into the conditions determining the annual or biennial habit.

Like the two other extensive sowings in the *Lamarckiana*-family this one also proved to be rich in mutants. I wish to call especial attention to this fact because I believe that the relative scarcity of mutants in the other branches of this family can be attributed to the small extent of the individual generations in these cultures.

I got altogether 41 mutants whose appearance in the various years and cultures I shall now put in the form of a genealogical table. This is constructed on exactly the same plan as the previous ones.

OENOTHERA LAMARCKIANA.

B

THE LAEVIFOLIA-FAMILY.

TABLE EXHIBITING THE ORIGIN OF NEW SPECIES FROM O. LAEVIFOLIA.

(The figures refer to the number of individuals.)

GENERATIONS	O. laevifolia	MUTANTS						O. Lamarckiana
		lata	elliptica	nanella	rubrinervis	spathulata	leptocarpa	
IX 9th generation 1895	—				44		5	
VIII 8th generation 1894		2			96			
VIII 1894	1500	2	1	0	2			
VII 7th generation 1893	—		1	2	—			
VI 6th generation 1892	—				—			
V 5th generation 1891	53	2	3		—			
IV 4th generation 1890	25				—			
III 3rd generation 1889	8	3	2	12	2	2		400
II 2nd generation 1888	2							—
I 1st generation Hilversum 1886–1887 (biennial)	—							

N. B. The numbers composing the generations marked with a — were not counted.

Let us now examine the origin of the various new species in this family a little more closely. We will begin with the 1889 crop. It comprised about 400 specimens of *Lamarckiana* and two rosettes and one annual plant of *O. lata.* But as I already had this species under cultivation I did not save them. Besides this, there were two rosettes of *O. elliptica* and two others of a new form, *O. spathulata,* which however I did not succeed in wintering. Dwarfs were fairly plentiful in this crop; two of them developed stems but did not succeed in flowering; ten remained in the rosette stage but only two of them survived the winter. These formed the stock of a *nanella*-family of which I have cultivated five generations, which will be described later (§ 18). One of the dwarfs that appeared in 1889 had the narrow leaves of *O. elliptica* but was a *nanella* in every other respect. It remained in the rosette stage but died during the winter.

Besides the mutations we have already named there occurred in the 1889 crop two examples of an entirely new form, *O. rubrinervis.* One of them stayed in the rosette stage and could not be wintered; the other developed a fine stem very early, bore a profusion of flowers which were however not enclosed in bags, and set a quantity of seed which was harvested on the 8th of October 1889.

These seeds were sown on the 5th of May 1890 on a small bed. The red-veined individuals were distinctly recognizable very soon after the seeds came up, and the rest were destroyed. In September I had forty specimens of *rubrinervis* of which nine flowered and set seed. The rest were either annual but not adult, or rosettes.

The seed saved in 1890 was used in 1891 partly for a culture on almost barren sand and partly for a control

culture on good soil. I allowed the latter only to flower and at the beginning of September chose the thirteen best specimens with red spotted calyces and red blush on the stalk, as seed-parents.

Since that time this species has maintained its characters. It has been left to pollinate itself and crossing has not, or has scarcely ever, occurred. Later, it was used for the development of a tricotylous race by weeding out all specimens which did not exhibit tricotyly. *O. rubrinervis* proved also to be almost completely annual, if suitably cultivated. In the first two years during which they were selected for tricotyly the 30-60 individuals which were raised gave rise to no mutants which need be mentioned here, but in 1894 there appeared among the tricotylous forms two examples of *lata,* both of which were annual and managed to flower; after which they were removed from the bed.

Since 1894 I have always enclosed the flowering spikes of the stock plants, i. e., plants which are chosen to provide seed for growing the next generation, in parchment bags and have artificially fertilized them with their own pollen in order to obtain definite proof of their constancy. It should be mentioned here that before this time these strains exhibited a very high degree of, though not an absolute, constancy. All that was necessary to show this was to grow the separate species on separate beds some feet apart.

The second main branch of the *laevifolia*-family arose, as I have already said, from the seeds of the smooth-leaved plants of 1888.[1] It began with two robust annual smooth-leaved plants. Next year I sowed their seeds on a small bed on which there flowered that summer

[1] See the table on page 273.

eight absolutely smooth-leaved individuals whose seed I harvested in autumn. There were no mutants.

In the following year (1890) I sowed the seed in a bed of about 3 square meters, and in the summer pulled up all the biennial plants as well as the younger ones of those that had produced a stem and those whose leaves were more or less crumpled. There were left, in September, 25 smooth-leaved individuals which however flowered late and set comparatively little seed. Still, I got about 25 ccm. of seed from them and was able therefore to continue the experiment in 1891 on a more extensive scale. It occupied, in fact, 14 square meters and mutants appeared again. There were two examples of *lata*, an annual one and a rosette, two feeble rosettes of *elliptica* and another *elliptica* which was so delicate that though it developed a stem, it soon died.

From this time I ceased to pay attention to the special peculiarity of this family, i. e., its smooth leaves, and used it for other purposes. The smoothness of the leaves however maintained itself (in spite of the fact that the plants were left exposed to the visits of insects) in the majority of the plants, the remainder being ordinary *Lamarckiana*. The experiments in question were discontinued in 1894, since when I have again got the family to breed true by employing artificial fertilization. But it did not mutate any more after that.

The experiments referred to above were three in number and will be briefly described here; I shall have to deal with two of them in greater detail later on. The object of the first was to breed a tricotylous race. This object was attained, although the first two generations were not so rich in tricotylous specimens as were those of the similar experiment referred to above, with *O.*

rubrinervis. But as I had not intended to go on with more than one of these two races I discontinued the experiment with this branch of the family after I had recorded the 1893 crop.

The object of the other two experiments was to breed a race with long fruits and one with short ones in order to find out the way in which this character responded to cumulative selection. (See Part III.) The long-fruited race gave rise to no mutants from 1892 to 1894 inclusive; the short-fruited race was, on the other hand, considering the relatively small extent of the experiment, extending, as it did, over from 4 to 6 square meters each year, fairly rich in mutants (see page 273). It gave rise, in 1893, to a beautiful rosette of *elliptica* and two dwarfs (an annual one and a biennial one); and, in 1894, to two annual *latas* which however had not succeeded in flowering by the middle of September; two *rubrinervis,*[1] a rosette and a weakly stem which did not flower; and, lastly, a rosette of *elliptica* which I did not succeed in wintering.

In conclusion I will remark that the tricotylous and long-fruited races referred to are excluded from the table on page 273, whereas the short-fruited race (1892-1894) forms the direct line of descent of the *laevifolia*-family.

In this family, therefore, there have appeared 41 mutations altogether, 13 in the main line of descent, 21 from *Lamarckianas* and 7 from examples of *rubrinervis.* This evening-primrose experiment occupied a relatively wide area in 1889 so that the characters of the young plants had more chance of developing than in previous years; this circumstance may, in part, account for the greater number of mutants that appeared that year. This

[1] See the table on page 273.

family originated from the seed collected near Hilversum in 1887. Since 1894 *O. lacvifolia* has always been artificially self-fertilized, and since that date it has ceased to mutate.

§ 7. TWO LATA-FAMILIES.

Oenothera lata is one of that group of my new species which have arisen most abundantly from *O. Lamarckiana*. It is also the oldest, appearing, as it did, as early as 1887 in my garden from the seeds gathered near Hilversum. In the following year it also arose from the seeds of the biennial plants which are mentioned in § 1 on page 220 as forming the first generation of my chief experiment.

From these two mutations I have derived two separate families, one of which I cultivated till 1890, whilst the other has with occasional interruptions been continued to the present day (1900).

Oenothera lata is, as has been already stated, solely female. If it is to bear seed it must be fertilized by other species. I fertilized it in 1887 with the pollen of *Lamarckianas* arising from the same sample of seed. From this cross I got in the following year some *latas* and some *Lamarckianas*, the former in the proportion of from 15 to 20 %.[1] From that time until 1894 I had the two forms growing together and left them to be fertilized by insects; since then I have enclosed the flowers of *lata* in parchment bags and fertilized them myself. The pollen I have used has either been from *Lamarckiana* with the same mothers as the *latas* in question, or from *Lamarckianas* of other ancestry.

[1] *Ueber erbungleiche Kreuzungen,* Ber. d. d. Bot. Ges., Nov. 1900, Bd. XVIII, p. 435.

I made the most extensive sowing, in these families, and the richest in mutations, in 1900; I shall deal with it first. In August 1899 I artificially fertilized 18 plants of *O. lata* in parchment bags, all with pollen of *O. Lamarckiana* which had either grown from *lata*-seed or were from pure race. In the spring of 1900 I sowed the seed, of each plant separately, in pans[1] and pricked out all the young seedlings, irrespective of their characters, into wooden boxes filled with manured soil. This was done as soon as the first leaves had completely unfolded and before the characters of any mutants that there might be were discernible. The seedlings remained in the wooden boxes until they had become strong young rosettes; and it was in these boxes that the mutants could first be recognized. Plate IV and figure 48 give an idea of the appearance of the boxes at this stage.

Plate IV is reproduced from a photograph which I took on the 18th of May 1900. The camera was so placed that its optical axis was vertical; all that then remained to be done was to push the box under the camera at the proper distance from it.

This plan obviated the necessity of tilting the box which might easily have fatal results for the young plants; and made it possible to grow them subsequently.

I dealt with over 2000 seedlings in this experiment. So that there was great opportunity for choosing good groups for photographing. I either chose groups including many examples of mutants of the same species (Plate IV) or groups comprising many different kinds of mutants (Fig. 48). I mention this because the figures

[1] My plan was to sterilize the soil in these pans by heating it, before sowing the seed, up to 90-100° C. This killed the seeds of weeds which the soil invariably contained. The soil was not manured. My seedlings did splendidly in soil sterilized in this way.

might give the impression that mutants are much more numerous than they really are. In this culture there were as a matter of fact 60 mutants among 2070 seedlings; that is—about 3 %. If I had wanted to show this proportion in the photographs each one could not have shown more than one mutation at the most. But the mutants are very irregularly scattered amongst the other

Fig. 48. Mutation in the *lata*-family (1900). Origin of *O. albida, O. oblonga, O. rubrinervis* and *O. subovata.* The plants are arranged in 3 rows as follows:

Upper row:	*Lam.*	*Lam.*	*lata*	*Lam.*	*rubrinervis*
Second row:	*lata*	*albida*	*albida*	*lata*	*Lam.*
Third row:	*Lam.*	*subovata*	*albida*	*oblonga*	*Lam.*

seedlings and I naturally chose groups in which there happened to be a lot of them. The most abundant mutation in this experiment as in others was *O. albida.* On Plate IV three are to be seen: the third plant in the upper row is one; another is the second plant in the third row; another the first plant (on the left) in the

fourth row. The plants are transplanted in rows in order to make the best advantage of the available space.

It should be observed that the pedigree of this culture contains seven successive generations of *lata*, the first of which arose from a *Lamarckiana* which I grew in my garden. This group arose from a single plant which was fertilized with the pollen of a plant of Lamarck's Evening Primrose of similar parentage. The origin of this race was therefore as pure as the unisexuality of *lata* permitted.

Seedlings of *O. albida* are very easy to recognize. Nothing short of seeing the plants themselves can really give an accurate idea of these phenomena: but the pictures may serve to convey the impression of the process of mutation. The plate shows besides *O. albida*, five plants of *O. lata* and six of *O. Lamarckiana*. The former can be recognized by their bright green round leaves, the latter by their darker green leaves which are more or less pointed. The three O. *albida* are much smaller, of a paler color, and with narrower leaves.

The plate shows another case besides these. I mean the plant at the right-hand end of the second row. It has narrow leaves and does not look quite like any of the types hitherto recognized in these experiments. Does it represent a new form? I devoted every possible care to its further cultivation; but it sickened and died before its mature characters had developed. The three *albidas* also got no further than the rosette stage.

Another group from the same experiment is faithfully represented by photography in Fig. 48. The group was taken in the way described above on the 25th of May; it arose from another parent plant, of the same experiment of 1899, which had likewise been fertilized

with the pollen of a closely related individual of *O. Lamarckiana.* There happened, in this group, to be four mutations so close to each other that they could all be photographed together: they did not occupy a space of

Fig. 49. *Oenothera rubrinervis.* A mutated specimen. It is the same plant we have seen in the right upper corner of Fig. 48, but now in flower. It originated from six generations of *O. lata* which in their turn arose from *O. Lamarckiana.*

more than 13 × 18 centimeters so that I could photograph them, natural size, on a plate of these dimensions.

The mutations depicted were *O. oblonga, O. rubrinervis, O. subovata,* of each of which there was one example, and *O. albida,* of which there were three. Besides these six *O. Lamarckiana* and three *O. lata* can be seen. The three *albidas* are easily recognized; they are Nos. 2 and 3 in the middle row and No. 3 in the lower. *O. rubrinervis* will be seen at the right of the upper row, easily recognizable by its narrow leaves; *O. subovata* and *O. oblonga* are Nos. 2 and 4 in the lower row.

These two were hardly old enough to be identified on the day they were photographed— especially the *subovata.*

Of the plants shown in Fig. 48 I kept one *O. lata* and all the mutants, planting them out on a special bed. The *O. lata* and *O. rubrinervis* produced stems and flowered in August, the rest behaved as biennials and remained in the rosette stage. When the example of *O. rubrinervis* flowered, and the characters of this species were developed to their full extent, I pulled it up and photographed it (Fig. 49) ; it was a very beautiful example of the rule that new species not only arise suddenly and without transitional stages from the parent species but with all their characters fully developed.

Of the *albidas* two died during the course of the summer, whilst the third together with the *O. oblonga* grew well into the autumn. The *O. subovata* was much damaged by the ravages of insects but managed to remain alive.

Another *O. oblonga,* which arose by mutation in the same experiment, developed a stem and flowered in August. Fig. 50 is a picture of it. It arose from the seeds of the same mother as the culture depicted in

Plate IV and grew in the same box quite close to the group that was photographed.

The 1900 crop contained, besides the mutants figured, a great many others partly of the same species and partly of others. The latter were three *O. nanella,* one *O. elliptica* and one *O. sublinearis.* This latter, which is one of my rarest species, I photographed, like the others referred to above, whilst it was flowering in August. I shall give the figure of it when I come to describe the species later on (see Fig. 85).

Fig. 50. *Oenothera oblonga.* An example which arose by mutation from the same parentage as the plant shown in Fig. 49.

In previous generations this family was very poor in mutations, for the simple reason that it was cultivated on a small scale. One year (1898) there arose in it, one example of *O. scintillans* and another year an entirely new form *O. semilata.* This looks very much like *O. lata* but is much more robust and bears plenty of pollen. It is one of my rarest new species, arising, as it did, only twice altogether.

On page 285 I give the genealogy of this whole fam-

ily. Its origin is the same as that of the main line of descent of the *Lamarckiana*-family referred to on page 224. The seeds of the nine biennial individuals of the period 1886-7, there mentioned, gave ten mutants: five

OENOTHERA LAMARCKIANA.

C

PEDIGREE OF THE FIRST LATA-FAMILY.

(The figures refer to the number of seedlings; the sign — means that this number was not counted.)

GENERATIONS		SPECIES							
		albida	nanella	*O. lata* + *O. Lam.*	oblonga	rubrinervis	sublinearis	elliptica	subovata
VIII	8th gen. 1900	42	3	2000	7	3	1	1	3
VII	7th gen. 1899			—					
VI	6th gen 1898			164		1 scintillans			
V	5th gen. 1897			—					
IV	4th gen. 1895			12 lata		1 semilata			
III	3rd gen. 1894			16 lata					
II	2nd gen. (biennial) 1888 1889	Lam.		5 lata		5 nanella			
I	1st gen. (biennial) 1886-1887	Lam.							

dwarfs and five *O. lata*; it is from these latter that the family in question arose. But in most years, as I have already stated, they did not mutate.

Let us now turn to the description of the second *lata*-family. This arose in my garden in 1887 from seeds which I took, in the preceding autumn, from a quinquelocular fruit of an otherwise normal plant of *Lamarckiana* growing in the field at Hilversum. Of these seeds not many germinated and, of the plants which arose from those which did, only five flowered in the first year in my garden; the rest were pulled up and thrown away. Of these five, two were *O. lata* and three *O. Lamarckiana*. The seed of the two former was harvested separately and sown in the following spring (1888) for the continuation of the experiment.

In 1887 no other *Oenotheras* flowered in my experimental garden besides the five individuals mentioned above. The *Lamarckiana*-family was flowering at that time in the Botanical Garden in a bed about 150 meters from my garden and separated from it by shrubbery. From the seeds of the two original *lata* plants there arose in April and May 1888, 614 individuals of which 21 % exhibited the *lata* characters. Towards the end of the summer I found that about one-third of the plants had remained in the rosette stage whilst two-thirds had developed stems. *Lamarckiana* and *lata* behave very much alike in this respect.

Of the annual *latas*, which could be fertilized by the rest of the plants up till the middle of September, I saved the best 39; whilst all the rest with a single exception I pulled up and threw away.

This exception was an example of *O. scintillans*, the first that occurred in my experiments. Its mother is therefore one of the *latas* of 1887, its father one of the three *Lamarckianas* of the same family. This *scintillans* was biennial, flowering and ripening its fruits

in 1889. Its seeds, some of which were sown in 1890 and some in 1894, gave rise for the most part to the same form. The culture of 1890 consisted partly of annual plants (10 of which were *scintillans*) and partly of biennial ones (comprising 26 *scintillans*), the former flowered well but too late; the others were frozen in the winter, so that I got no seed from this experiment. The 1894 crop was entirely biennial and contained 11 plants of *scintillans* which set seed in 1895.

Let us now return to the main line of descent of our family. On the 18th of April 1889 I sowed the seed which had been harvested, on a bed (about 3 square meters in size) which was fairly thickly covered with plants towards the end of May when the *latas* could easily be distinguished from the *Lamarkianas*. Most of the latter were removed. Towards the end of July, 12 annual specimens of *lata* flowered: the rest of the *latas,* which had either developed stems too late or still remained in the rosette stage, were weeded out. Of those that flowered eleven set seed, and were harvested together.

Part of the seed was sown in the following year; a smaller sample was kept till 1894, in which year they gave rise to 340 seedlings of which 52 were *lata*: these were however not cultivated further.

I sowed the seed to produce the fourth generation on the 5th of May 1890; as before, on a bed of about 3 square meters. At the beginning of July there were on this bed 79 specimens of *lata* and many of *Lamarckiana*. The former were partly annual, partly biennial. The annual plants did not flower before the middle of September and only six *latas* set seed which ripened very late and could not be harvested before December.

The 1890 crop contained, besides the two parent types, three mutations, viz., one *elliptica* and two *spathulata* which however did not flower and were not cultivated further.

Mention must here be made of a *Lamarckiana* in the 1889 crop, in some of the flowers of which the tips of the sepals had become broad and the sepals themselves

OENOTHERA LAMARCKIANA.

D

PEDIGREE OF THE SECOND LATA-FAMILY.

(The figures refer to the numbers of seedlings.)

GENERATIONS		SPECIES				
		elliptica	Lamarck-iana	lata	spathulata	elliptica
V	5th generation 1890	1	Lam.	3 lata	lata 2	1
IV	4th generation 1889		Lam.		lata	
III	3rd generation 1888		Lam.		lata	1 scintillans
II	2nd generation 1887		3 Lam.		2 lata	
I	1st generation Hilversum 1886		Lam.			

leaf-like. I sowed the seeds of this plant, but the abnormality was not repeated: there were however among its offspring 3 *latas* and one *elliptica*. The experiment was not continued.

For the next three years (1891-3) I did not cultivate either this or the other *lata*-family, on account of the difficulties of fertilization. In 1894 I took it up

again and sowed the 1890 seed. It gave 20 examples of *O. Lamarckiana* and 6 of *lata*—only 26 seedlings altogether. The 6 *latas* were annual, flowered well, and provided material for an investigation, to be referred to later, into the sterility of the pollen.

The foregoing account can be summarized in the table on page 288.

The question naturally arises whether the mutability in this family comes from the father or from the mother. I believe from the father because my new species have as a rule bred true and at any rate have mutated much less than *Lamarckiana* itself. On the other hand it seems probable that crossing in itself favors the production of mutations.

§ 8. MUTATIONS IN OTHER FAMILIES.

Mutations have also occurred repeatedly in cultures of *O. Lamarckiana,* which have not yet been described. It may almost be said that every extensive sowing will give mutations; provided that the plants are not grown so thickly that the majority of them are prevented even from showing their characters; and provided that the beds are carefully examined. For before a plant begins to develop a stem it forms a rosette with a radius of some 20 to 30 centimeters, and there is not room for many flowering examples on a bed—20-40 at the most per square meter.

My mutations were almost always, at any rate in their young stages, more delicate than the parent species so that they were very liable to be crowded out.

I propose, therefore, now to say something about the methods of cultivation, and about the search for muta-

tions with especial reference to the characters of the young plants.

I shall describe these characters in greater detail in the following chapter, but it seems desirable to preface it by a short comparative résumé.

I began by sowing the seed in the garden. The result of that was, as I have already mentioned, that part of the seed remained in the ground and germinated in subsequent years. So that each particular part of the garden could only be used once. I therefore adopted the plan of sowing the seed in pans; the soil for them was bought from a nursery and was sterilized so that any seeds of *Oenothera* that happened to be in it were destroyed—a fact completely proved by numerous control experiments. The seedlings remained in these pans when ever possible, until they were old enough to be identified, and until the different kinds had been recorded; if this was not possible they were transplanted into wooden boxes measuring 30 by 50 centimeters and 10 centimeters deep. They remained in these until they could be planted out in the beds.

The plants were only grown in pots when it was desirable that they should be treated particularly carefully or when especially robust plants were wanted.

A sharp distinction is to be drawn between crops which are intended to flower and such as are recorded and thrown away before the plants develop stems. The former are almost always transplanted from the pans before the characters of the new species are recognizable; the latter are very often kept in the pans until they are done with.

Some forms are recognizable as soon as the first leaves are developed. This is almost always true of *O.*

lata and very often, especially if the seeds are not sown too thick, of *O. nanella*. *O. albida* can also be recognized very early. *O. oblonga* and *O. rubrinervis* often cannot be identified until much later: and *O. scintillans* later still. In fact it was quite an exception when I recognized one of the last named in the pans at all with sufficient certainty: when they were being transplanted they were, commonly, simply taken for weak plants.

Fig. 51. A mutation in a seed-pan. The plant in the middle is an *O. lata* mutant. The whole culture arose from a cross between *O. Lamarckiana* and *O nanella*, to which two types all the rest of the plants in this figure belong.

The superficial area of soil contained in these pans is 25 × 25 centimeters. From ⅓ to ⅔ cubic centimeters of seed is sown in them. Under these conditions the plants have ample room when they are young. But if they grow to an age at which the mutants amongst them are recognizable they become much too thick for it to be

possible to photograph them. This can only be done when few seeds are sown, or when few germinate.

Fig. 51 shows an example of such a case. The seeds sown were the result of a cross. *O. Lamarckiana* was crossed with *O. nanella* in August 1899; about 250 of the seeds germinated and about 30 % of the plants they gave rise to were *O. nanella*. It is easy to distinguish, in the figure, between the loose rosettes of the parent species and the rosettes of the dwarf by the fact that in the latter the central leaves are more closely packed. Right in the middle there stands rather alone one *O. lata* easily recognizable by its round (as opposed to pointed) leaves. It was rather covered by its neighbors, so before photographing it I put its leaves over those which were covering it. Otherwise nothing in the group was interfered with.

The two parents crossed were of pure origin; the *Lamarckiana* came from the main line of descent of my experiment (after eight generations of cultivation) the *nanella* arose from this *Lamarckiana* race in 1895 and had since bred true for five generations. The *lata* in Fig. 51, therefore, had no ancestors of a like character at any rate during this period (1886-1899). In the lateral branches of this pedigree however, this form has arisen almost every year.

The characters of the young plants can be most clearly apprehended for the purposes of identification, from the figures of the rosettes which will be given later. Meanwhile I propose to describe here the typical form of the adult leaves of the rosettes of the various forms (Figs. 52 and 53). The leaves are photographed one-half the natural size and were taken from the plants in the wooden boxes at the beginning of June. The cultures

were pure, that is to say each species in each culture was raised from seeds of that species: this made it easy to choose a good average form of leaf.

The most easy to recognize are *O. nanella* (Fig. 52*n*) and *O. lata* (Fig. 52*l*). The former has rather short-stalked slightly undulating leaves with broad bases; the result being that the leaves have the appearance of being

Fig. 52. Fully grown leaves of young rosettes in June. *L, Oenothera Lamarckiana; n. O. nanella; g, O. gigas; r, O, rubrinervis; l, O. lata; s, O. scintillans.*

much crowded in the heart of the rosette. The latter has long-stalked leaves whose apices are quite round. Their surface is very uneven but their margin is fairly level and tears very easily if one attempts to press the leaf flat (hence the small tear at the tip). *O. gigas* is

distinguished from *O. Lamarckiana* by its much more robust and still broader leaves (Fig. 52 *g* and *L*). *O. rubrinervis* (Fig. 52 *r*) and *O. scintillans* (*s*) have narrower leaves, those of the former being gray-green, those of the latter dark green, whereas the surfaces of the leaves of both these forms are hardly crumpled at all. *O. albida* (Fig. 53 *a*) and *O. oblonga* (*o*) are scarcely recognizable at this age by the form of their leaf. *O. albida* varies very much according as whether one is dealing with the ordinary weakly forms or with plants which have grown up strong as a result of special care. The leaves of the former are small and narrow, pale green and often even almost white; those of the latter are chiefly recognizable by their pale color. *O. oblonga* has leaves with very broad main veins: this breadth is much more striking on the upper than on the lower surface which is the one figured. They are pointed and, when the plants are young, broad; but later they become very narrow.

Fig. 53. Full grown leaves of young rosettes in June. *a, O. albida; o, O. oblonga.*

For comparison with the leaves of the young plants there are shown in Fig. 54 the grown leaves of flowering plants. The leaves were plucked from the plants just below the first flower-bearing nodes. They are the same species as those whose seedling leaves have already been figured, with the exception of *O. lata*, *O. Lamarckiana* and *O. nanella*.[1]

[1] I have copied these leaves photographically by spreading slightly faded ones out on sensitized paper and then printing under glass in an ordinary printing frame. I then photographed the prints, reducing them to about one-half.

The leaves of *O. gigas* are recognizable by their greater breadth; all of the others that are figured are narrower than *O. Lamarckiana.* The leaf of *O. oblonga*

Fig. 54. Leaves from the stems of flowering plants of *g, O. gigas; r, O. rubrinervis; o, O. oblonga; a, O. albida; s, O. scintillans.*

is characterized by its broad median vein; that of *O rubrinervis* is slightly more pointed than *gigas* and *oblonga*; moreover its surface is usually very uneven. But,

the leaves of these three types, *oblonga, albida* and *scintillans*, can really only be distinguished by their color and substance.

The various new species (with the single exception of *O. leptocarpa* which is not recognizable until it flowers) can, however, be recognized with certainty at any stage in their development by their leaves. All the later characters, the form of the flowering branches and of the flowers themselves, in *O. lata* the absence of pollen, the size of the fruits and the abundance of seed—can be predicted from the leaves, if the species in question has once been seen in flower and fruit. But, as a matter of fact, I have planted out every year, for further growth, a greater or smaller number of the plants which had been sorted by their seedling characters; and in no case has my identification proved to be erroneous.

I have sought for mutants among the crops from *Oenothera* seeds as often as possible by this method. Whether, and in what quantities, they appear depends in great measure, as I have already said, on the extensiveness of the sowing. But these things are undoubtedly influenced by other causes operating during germination (see p. 263) or fertilization or even earlier.

As a rule the new species proved much less mutable than the original *O. Lamarckiana* from which they originated. It is only the inconstant forms amongst them which exhibit a very high degree of mutability, as for example *O. scintillans*.

The power to mutate is maintained after crossing and in cases where the original form *O. Lamarckiana* reappears out of a cross it does so with its full—I had almost said normal—capacity for mutation.

One of two instances will serve to exemplify these generalizations here. I shall reserve a more complete proof of them until I come to the description of the separate new species.

Pure sowings of *O. leptocarpa, O. nanella* and *O. oblonga* gave rise solely to their own type with the exception of the following mutants. Subjoined is a list of these, together with the date of the experiment and the number of the seedlings.

MUTANTS ARISING FROM NEW SPECIES.

SPECIES	DATE	NUMBER OF SEEDLINGS	MUTANTS
O. leptocarpa	1896	500	2 *nanella*
O. nanella	1897	760	1 *oblonga*
O. oblonga	1897	2150	2 *albida*
			1 *elliptica*
			1 *rubrinervis*
	Total	3410	7 mutants

That is to say a proportion of about 0.2 %, whereas *O. Lamarckiana* usually has 1-3 % and often more mutants.

O. scintillans is an example of an inconstant new species in as much as often only about ⅓ of its offspring are *scintillans* (see p. 245); the two remaining thirds are composed of partly *O. oblonga* and partly *O. Lamarckiana* and, to a much less extent, of the two other common species *O. lata* and *O. nanella.*

I found the following numbers of these in the experiments with *O. scintillans* in which the seeds were set on typical plants which had been fertilized by their own pollen.

MUTANTS ARISING FROM O. SCINTILLANS.

DATE	NUMBER OF SEEDLINGS	LATA	NANELLA
1896	268	8	1
1897	572	3	3
1898	447	1	0
1898	587	3	2
1899	148	2	0
1899	5850	21	23
Totals	7872	38	29
		67	

That is, roughly 1% or about as much as in the case of *O. Lamarckiana* itself.

A parallel result is got with crossings. From these there arise the two parent forms and very often *O. Lamarckiana* itself, even when it was not one of the parents.[1] But other mutations occur as well, as the following instances will show.

MUTANTS ARISING FROM THE CROSS O. LAMARCKIANA × O. NANELLA.

DATE	NUMBER OF SEEDLINGS	ALBIDA	LATA	OBLONGA	RUBRI-NERVIS	ELLIP-TICA
1897	1341	1	7	20	—	—
1897	1051	—	5	12	2	—
1898	474	—	2	5	—	—
1899	3815	—	3	1	—	1
1899	1606	—	5	—	—	—
	8283	1	22	38	2	1

Altogether 64 mutants, or nearly 1 %.

[1] See *Ber. d. d. Bot. Gesellschaft,* Bd. XVIII, 1900, Heft X, p. 435.

MUTANTS ARISING FROM THE CROSS O. LATA × O. NANELLA.

DATE	NUMBER OF SEEDLINGS	ALBIDA	OBLONGA	RUBRINERVIS
1895	63	—	—	1
1897	837	6	7	—
1898	101	1	1	—
1898	146	—	3	—
1899	280	5	3	—
1900	159	3	—	1
	1586	15	14	2

Altogether, 31 mutants, or nearly 2 %.

MUTANTS ARISING FROM CROSSES WITH THE OLDER SPECIES.

NATURE OF CROSS	DATE	NUMBER OF SEEDLINGS	MUTANTS
O. Lam. × *O. biennis*	1896	30	2 *oblonga*
O. Lam. × *O. biennis*	1900	80	1 *lata*
			1 *nanella*
O. Lam. × *O. suaveolens*	1897	200	8 *oblonga*
			1 *elliptica*
O. lata × *O. biennis*	1899	299	2 *nanella*
			1 *scintillans*
O. lata × *O. suaveolens*	1900	743	13 *albida*
	Totals	1352	29 mutants

That is, somewhat over 2 % of mutants.

The mutability of all these crosses is thus shown to be about the same as that of *O. Lamarckiana.*

I have, finally, tested the offspring of crosses in the second generation. If we select the seed of hybrids which, to judge by their characters, belong to some one of the new species, we get, by sowing it, proportions of mutants which closely correspond with those given on p. 297. But if we select the seed of self-fertilized hybrid *Lamarckianas* we find, on the contrary, that they exhibit the same degree of mutability as ordinary ones.

MUTANTS ARISING FROM PLANTS OF LAMARCKIANA WHICH HAVE THEMSELVES ARISEN FROM CROSSES.

Experiments Carried Out in 1898.

CROSSINGS IN 1896	NUMBER OF SEEDLINGS	MUTANTS IN 1898 *albida*	*lata*	*nanella*	*oblonga*
O. Lam. × *O. nanella*	1063	1	—	5	2
O. lata × *O. Lam.*	427	—	3	—	2
O. lata × *O. nanella*	1693	1	1	12	1
" " " " "	390	—	1	6	1
O. lata × *brevistylis*	1026	—	2	3	2
Totals	4599	2	7	26	8

That is, altogether 43, or about 1 % of mutants.

We may sum up by saying that we never find any more than slight deviations from the original degree of mutability exhibited by *O. Lamarckiana.* It seems to retain this property through all generations and in spite of crossing; at any rate in the course of my experiments. In the new species, on the contrary, this capacity for mutation is modified; for it is a constant feature of them that their mutability is much diminished. It has, however, not completely disappeared, and the power of giving rise to the same new species as does the parent form has been evidently transmitted to them.

§ 9. MUTATIONS IN NATURE.

The object of the experiments in my garden was not to induce mutations, but to make a closer study of the process of mutation than was possible in nature.

Of course, I regard the induction of mutations as a much bigger problem the solution of which I would gladly have attempted. But I soon saw the necessity of an exhaustive preliminary investigation. An exact knowledge of the way in which new species arise in nature

seemed to me to be an indispensable preliminary. Hitherto this phenomenon had not been observed at all, in the natural state. I had to postpone the plan of determining the causes of these processes. Then it must be remembered that our knowledge of the effects of crossing was at that time practically *nil*; and such knowledge is an absolutely essential condition for an experimental investigation of the phenomenon itself. It was imperative that the laws of hybridization (especially those to which the *Oenotheras* conform) should be determined first.

For these reasons I have postponed an investigation into the causes of mutation until these preliminary problems were well on the road to solution.

There are two ways of studying mutation in the field. The first is to look for and collect the mutants in the place where the parent grows. The second is to collect the seed in the field and to grow it under as favorable circumstances as possible.

It will be immediately evident what an incomplete method the first one is, and how much superior to it is the second. For the mutation must obviously already have taken place in the seed; all that germination does is to bring it before our eyes. Consider what a vast number of seeds perish during the first few days after germination, or even during the first weeks, when they are left to nature; especially in the case of the weaker seeds, which perhaps may contain the greater number of the mutants. An average plant of *Oenothera Lamarckiana*, growing wild, often has over a hundred fruits and each fruit contains from one to two hundred seeds. Therefore even in times of rapid multiplication it is only a very small percentage of the seedlings which grow to

their full stature. So that even if the plants do give rise to ever so many mutations in their seeds, there is always the possibility either that there will be no sign

Fig. 55. *Oenothera Lamarckiana.* An entire plant with flowers on its main stem and lateral branches.

of them or that traces of them will only be discovered from time to time.[1]

A simple and certain method of discovering whether

[1] *Sur l'introduction de l'Oenothera Lamarckiana dans les Pays-Bas.* Nederl. Kruidk. Archief, Aug. 1895.

a given species in a certain locality is in a mutable condition is to collect its seeds and sow them. The sowing should be carried out on a large scale. A whole series of experiments, which I have started with a number of different species with this end in view, have been without any positive result. From which I conclude that mutations in nature are rare; although I am convinced that they will be found from time to time if they are carefully looked for.

I have for many years applied both these methods to the case of *Oenothera Lamarckiana*. I have visited the field itself almost every year, or, if not, have had it visited by others. The majority of the new forms have been observed in that way, but usually as weak seedlings or young rosettes; and very rarely indeed in flower. Furthermore I have collected seed in the field, especially in the period 1886-1888, when I began my experiments, and have sown it in my experimental garden; in the first two years in small quantities, but in the last one on a large scale. Since then I have repeated the experiment from time to time and only stopped when I was pretty certain what would happen.

I shall now give a list of the various species which I either found in the field at Hilversum or raised from seeds which I collected there.

Oenothera lata. In 1887 I raised three examples of *lata* which were all annual from seeds which I gathered in the autumn of 1886 from quinquelocular fruits of otherwise normal *Lamarckiana* plants. Two stayed in my garden and gave rise to one of the *lata*-families described in § 7 (p. 288); the third germinated with three cotyledons and was transplanted to a garden near Hilversum where it flowered but did not set fertile seed.

In the autumn of 1888 I raised in my garden, from seed gathered from apparently normal examples in the field, besides numerous *Lamarckianas* seven examples of *lata*; of which four developed stems, one remained in the rosette stage, whilst the two others did not come up till late in the summer. In the same summer I found a beautiful flowering specimen of *lata* in the field and one or two other young plants which were immediately recognizable as belonging to this new species.

In 1894 two flowering plants and one rosette of *lata* were again found in the field.

O. elliptica. I found one rosette in 1886 and another was found in 1894.

O. nanella was obtained in 1889 from seed collected in the field in the previous autumn: there were three rosettes which however did not survive the winter. One of these was a *lata-nanella*; that is to say it combined the characters of both forms, a phenomenon which has occurred again in my experiments. Another dwarf was found in the field at Hilversum in 1894.

O. rubrinervis. One rosette was raised from the seed collected in 1888, which has been so often referred to already.

O. spathulata. This form was collected as a rosette in the field at Hilversum in 1886 and 1894.

Five of the new species therefore, either appeared in the field at Hilversum or from seed collected there. They appeared rarely, but repeatedly, and moreover their appearance extended over the course of several years. It was, however, not possible for the ones that arose later to have descended from the earlier ones, since the latter had not flowered.

The foregoing account may be summarized in the following list.

SUMMARY OF NEW SPECIES FOUND AT HILVERSUM.

PLANTS		FROM SEED	
O. lata	1889, 1894	*O. lata*	1887, 1889
O. nanella	1894	*O. nanella*	1889
O. spathulata	1886, 1894	*O. lata-nanella*	1889
O. elliptica	1886	*O. rubrinervis*	1889

This list contains just those forms which are the most easily recognizable and appeared oftenest in my cultures. Of the rest the only one which has occurred in my garden up to the year 1894, (the last year in the above list), was *O. scintillans* and this only in one specimen.

These forms therefore clearly originated in the field and not in my cultures. Moreover they arose there in the same way as in my experimental garden, without transitional stages, from the seeds of normal *Lamarckiana,* and year after year.

These observations do not pretend to be complete but they suffice to demonstrate the identity of the processes in the field and in the garden. The cultures are merely a more convenient and certain method of discovering what happens in nature.

Whether *O. scintillans* and the other species which were only observed in my garden also appeared from time to time in the field at Hilversum, I do not, of course, know. But I regard it as extremely probable that they did. Several of them appeared so rarely in my garden that it did not seem worth while to try to get them again by carrying out more extensive sowings. Still less did it seem likely that I could get them by sowing seed collected in the open.

There is no reason to suppose that the first record of a new species corresponds with its first appearance. I found *O. elliptica* and *O. spathulata* the first year that I visited the place (in 1886); I found *O. lata* the year after. It is very probable indeed that these and other forms have also appeared in previous years either as young plants or as seeds.

I am convinced that the mutations of our Evening Primrose were already in full swing when I began my observations and experiments, and that I did not catch it in the act of beginning to give rise to new species. I simply discovered how the new forms, which though in a latent condition were already there, came to light from time to time.

The beginning of the process of the origin of a new species will escape observation so long as it is impossible to induce mutations at will. And it is not likely that we shall be able to do that for a long time.

The fact that two subspecies already existed at Hilversum in 1886 in full development speaks strongly in favor of the view that *O. Lamarckiana* was at that time already in a mutable phase. The two species I am referring to are the *O. laevifolia* and *O. brevistylis*. In 1886 I found two examples of the latter in flower; the former I found in the same year as rosettes which flowered in 1887 and provided the seed for the *laevifolia*-family described above. Inasmuch as these two new species had not been observed anywhere else it is reasonable to believe that they arose on the spot. This view is supported by the circumstance that I first found only a few examples of each of the two species, each in a little group to itself; *O. laevifolia* in the northwest, and *O. brevistylis* at the northeast corner of the field. Whether

they had arisen a short or a long time back cannot be determined now. That they were able to maintain themselves, whilst the other species were not, is probably due to the fact that during the seedling and rosette stages they are not in any way inferior to the ordinary Evening Primrose.

And, lastly, the question arises whether the mutation period which I observed, began in the field at Hilversum or before.[1] The rapid multiplication of the plant in the field since it was first sown in 1870 would appear, according to horticultural experience, to be a sufficient cause of mutation. Within about 8 generations (1870-1886) the plants had increased from one or two to many hundreds which had scattered their seeds far and wide.

Perhaps the mutation period was much older, if not in the case of all the new forms at least in that of those which appeared oftenest (for example *O. lata* and *O. nanella*). But as I did not witness the beginning of this process it does not seem to me to matter much when and where it happened.

The point is that the cultures in the garden disclose to us what happens, but ordinarily escapes observation, in nature.

[1] Later experiments have shown the mutation period to be much older. Cf. *Ueber die Dauer der Mutationsperiode bei Oenothera Lamarckiana, Ber. d. d. bot. Ges.,* 1905, Bd. XXIII, p. 382. (Note of 1908.)

II. THE ORIGIN OF EACH NEW SPECIES CONSIDERED SEPARATELY.

A. THE TWO OLDER SPECIES.

§ 10. OENOTHERA LAEVIFOLIA.

The reader will remember that amongst the Evening Primroses in the field at Hilversum there grew two new species, *O. laevifolia* and *O. brevistylis*. These forms have not been observed anywhere else before, so far as I have been able to ascertain. It follows that they must have arisen either on the spot (that is after 1870) or at some period before the introduction of the parent species. They have maintained themselves in the locality ever since I began to observe them but there are no means of telling whether a race of them has existed since they first arose, or whether they have been produced by the *Lamarckiana* from time to time.

They have never arisen in my cultures. I have spent much labor in looking for them; but in vain. *O. brevistylis* cannot possibly be missed if it is there and I have carefully searched the plots for *O. laevifolia*. For example in 1895 I looked through over one thousand flowering plants of the *Lamarckiana*-family without seeing a trace of a smooth leaved form. I repeated the search in later years when I had many thousands of flowering *Oenotheras* under cultivation.

I have often brought *Oenothera laevifolia* from Hilversum to Amsterdam, sometimes in the shape of seeds, sometimes by fertilizing castrated flowers of my *O. Lamarckiana* with *laevifolia* pollen. From the seeds ripened at Hilversum I obtained in 1888, for example, no more than 2 % *laevifolia*; in 1895, on the other hand, about 50 %. The former number is obviously the result of the rarity of the species in question at that time, there being little chance of its being fertilized by its own pollen.

Fig. 56. *Oenothera laevifolia.* Top of a stem, in flower.

The distinguishing features of this species are to be found partly in the leaves and partly in the flowers.

The leaves of *Oenothera Lamarckiana* are rather coarse, an effect produced by the numerous crumples which distort the areas between the veins and especially those areas which border on the middle region of the principal veins. They are caused by a faulty correlation between the growth of the areas and of the veins; either the areas grow too fast, or the veins elongate too slowly.

My *O. laevifolia* does not possess these crumples; the leaves are almost flat and appear therefore of a more beautiful and uniform green. They are rather narrower and as a rule somewhat smaller than those of the parent species, although the difference is so trivial that it falls within the limits of individual variation. This indicates that the absence of crumpling is due to a diminished growth of the areas between the veins.

Such crumples occur not only in *O. Lamarckiana* but in some of the new species that have arisen from it, for example *O. lata* and *O. albida.* I have therefore figured transverse sections of these leaves in Fig. 57 as being the best way of giving an idea of the extent of these crumples.[1] The leaf of *O. Lamarckiana* is just like that of *O. albida* in this respect whilst the leaves of *O. lata* are distorted much more (Fig. 58). The leaves of *O. laevifolia* appear in transverse section as a straight line from which the nerves project here and there.

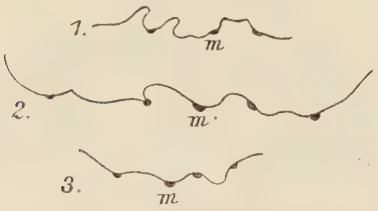


Fig. 57. Transverse sections of leaves to show the crumples. $^2/_3$ nat. size. 1, Part of a leaf of *O. lata.* 2, Transverse section through whole leaf of *O. lata.* 3, The same of *O. albida.* *m,* median veins.

Incomplete development of this character occurs fairly often in *O. laevifolia* even after many years of selection. A smooth-leaved plant is occasionally met with posses-

[1] To make these figures as faithful as possible I have embedded the fresh leaves in a thick slab of glycerin-gelatin, and when this had hardened cut them in it. I took a section of about 1 cm. thick and laid on it a dry film of gelatin on which I traced the outline of the section of the leaf. If I had simply cut strips from the leaf or had tried to deal with thinner sections, many of the crumples would inevitably have disappeared.

sing occasional crumples on its leaves and sometimes whole leaves covered with them. Or again the smoothness of the leaves gradually decreases from the top of the stem downwards. It even happens sometimes that it is impossible to draw a sharp line of demarcation between *Lamarckiana* and the smooth leaved plants, or to calculate the percentage of the latter.

Fig. 58. Radical leaf of a rosette of *O. lata*, viewed from the dorsal side, to show the numerous unevennesses (crumples) on its surface.

When it was possible to allow not merely the main stem of the plant to grow (which was all I could do as a rule, through lack of space) but also the lateral branches which spring from the axils of the radical leaves it was found that the *laevifolia*-characters were better developed in the leaves of the branches than in those of the main stem. In such cases these were often useful in identifying the plant.

O. laevifolia has obviously inherited the occasional crumples which it possesses, from its parent species; they can be regarded as rudimentary or atavistic characters.[1] Closer study will probably prove such relics to be much commoner in nature than

[1] Like the stalked leaves of the young plants of *O. nanella*. See § 18 and the tables in § 27 of this part.

is generally supposed. They belong to the same category as DELPINO'S subvariations.[1]

These crumples occur in many other plants. They are sometimes regarded as useful adaptations. "The more the form of the leaf surface is adapted for retaining water resulting from rain or thaw by trough- or cup-shaped depressions in its surface," says VON RÜMKER,[2]

Fig. 59. *Oenothera laevifolia.* Flowers with narrow petals; *a,* seen from the side; *b,* seen from above; *c* and *d,* isolated petals spread out. In *a* one of the petals has been removed. *a, c, d* taken in 1894, *b,* in 1899.

"the longer can the plant keep the water for its own use." How far *O. laevifolia* is inferior to other Evening Primroses from its lacking these depressions is not an easy question to answer; but this much is certain that I have always found it weaker and smaller than the parent species. In the experimental garden however where the

[1] The deviations from the type of leaf, characteristic of the species, which often occur at the bottom of branches are classified by DELPINO as subvariations. See DELPINO, *Teoria generale della Fillotassi,* 1883. They are often of an atavistic natur

[2] VON RÜMKER, *Zuckerrübenzüchtung,* 1894, p. 6.

plants never lack water this character makes no difference.

A very characteristic feature of *O. laevifolia* is afforded by the flowers on the weaker shoots. They have narrow petals which exhibit every transition from the broad, obcordate contour of those of the strongest flowers to oval or elliptical forms as shown at *c* and *d* in Fig. 59.

This character is very constant. It was through it, that I first discovered the new form and it was only after this had been in cultivation for some time that I became acquainted with the smooth leaves. Weak plants bear such flowers on the main stem; stronger ones either on the whole extent or only at the base of the lateral branches.

In the height of summer these flowers are rare; but towards autumn and often as early as the beginning of September they appear in greater numbers. By cultivating only healthy plants without lateral branches it would be possible for a whole year to go by, without seeing one of these flowers: this has sometimes happened in my experiments.

There is something extraordinarily attractive about these flowers. They are smaller and neater than the rather gross and stout flowers of the common Evening Primrose; their color is often paler; their form, in a sense, freer, inasmuch as the petals scarcely touch one another. I have often stuck them into my journal or photographed them. I have found them from 1887 up to the present day, always the same, exhibiting the same varieties of form but without progressing in any one particular direction, just like all the other new species which have proved constant in all their characters from their origin.

The forms of the petals of a single flower often differ from one another (Fig. 59 *b*). The petals of plants grown in the field on dry sand were narrower than those of plants grown in the garden on manured soil. The petals of the former were almost twice as long as broad, in those of the latter the relation of length to breadth was as 2 to 3. The emarginate character of the normal petals is absent in them; the petals are, on the contrary, obtusely rounded. Their greatest breadth is in the middle. The narrowest petals that I have observed were three centimeters long and one broad. But as I have already stated there exists a complete series of transitions between these and the obcordate ones of strong flowers.

Oval petals are by no means confined to *O. laevifolia.* They occur regularly on *O. elliptica.* I have also sometimes found them on weak shoots of *O. biennis.*

In the other characters *O. laevifolia* is very much like *O. Lamarckiana,* not differing from it in any essential features save those already mentioned. The plants are about the same size. So are the flowers and fruits and general habit. Nevertheless a bed of *O. laevifolia,* even if it is some distance away can always be recognized from a group of *Lamarckiana* by characters which may be manifested to a greater or lesser degree but which always tend in the same direction. The color of the flowers, especially of the later ones, is usually a little paler; the buds a little thinner, the bracts of the inflorescence a little narrower and the whole plant more delicate and neat.

During the first few years of its cultivation I used to allow *O. laevifolia* to cross freely with *O. Lamarckiana* for reasons which I have mentioned above (§ 6). But since 1894 I have excluded the visits of insects by en-

closing the flowers in parchment bags; and fertilized them with their own pollen. Since that time the species has proved absolutely constant; and each year I choose the best examples with the smoothest leaves as seed-parents.

§ 11. OENOTHERA BREVISTYLIS.

This form has been thoroughly investigated and described by JULIUS POHL.[1] I have used it mainly in hybridization experiments, in which it behaves in a different way from all other species in the group of the evening primroses. I shall deal here only with its external characters, with its first discovery in the field and with its constancy. This species, which is very easily recognized during its flowering period, has never arisen in my cultures.

In the rosette stage and in fact at any time before it flowers, it is difficult to distinguish. Its more rounded leaves give it a slightly different appearance; and in hybrid cultures it is often possible before any stems have been developed to predict whether there will be many or few *brevistylis*. But it is not until the flower buds appear on the stem that the difference between it and other forms becomes clearly discernible, and that one can record them with safety. The young inflorescence forms a rosette of rounded leaves on the top of the stem in *O. brevistylis* and of pointed ones in *O. Lamarckiana*. Shortly afterwards the buds appear; they are shorter, thicker and blunter than the slender conical ones of the parent species. Then the flowers open, just as large and just as beautiful as in Lamarck's Evening Primrose. At first sight it looks as if they had neither a style nor stigma;

[1] JULIUS POHL, *Ueber Variationsweite bei Oenothera Lamarckiana*, Oester. bot. Zeitschrift, Jahrgang 1895, Nos. 5 and 6, Tafel X.

but closer inspection reveals them hidden away in the tube at the base of the corolla. Hence the name *O. brevistylis* or short-styled Evening Primrose. The length of the style varies very much; the stigmas sometimes lie right inside the tube, sometimes they stand a full centimeter out of it. But there is a great gap between the longest styles of *O. brevistylis* and the shortest ones of *O. Lamarckiana.*

When the flowers are through blooming they wither down as far as the fruit but are not thrown off as they are in *O. Lamarckiana,* but remain attached for considerable time to the unripe fruit. The plants can be recognized from afar by this character, and even perhaps still more readily by the smallness of their fruits. In their fully developed state these are hardly larger than the ovaries of open flowers; they remain bent outwards, pressed against the bract and almost hidden between the broad auricles at its base. From a distance it looks as if the plant had never been fertilized: *Lamarckiana* on the other hand does not hide its great, fine, erect fruits between the bracts. (Plate I.)

In the fruiting period *Brevistylis* plants can therefore be more easily recognized than those in blossom; but as a rule *brevistylis* keeps up flowering later into the autumn than *O. Lamarckiana.*

The stigmas are developed in an unusual way; for instead of being stout and cylindrical they are flattened and leaf-like. They retain the abundance of pollen that is brought to them by humblebees, permit the development of pollen tubes which elongate in the usual way, and reach the ovary in numbers but fertilize only very few ovules. Many plants set no seed at all, others very little.

The ovary extends a little above the insertion of the corolla up into the style.

O. brevistylis was the first sub-species of *Oenothera Lamarckiana* which I discovered. I found it in August of the first year of my investigations, 1886, when, as already stated (p. 266) it occupied a little corner in the northeast of the field. There were two individuals, one where the plants grew thickest, the other on a spot about one hundred paces away. Both were well developed, flowering from many shoots and, as far as I could judge, biennial. I found them on the 25th of August. They caught my eye from quite a distance by the almost complete absence of any fruit on them. This character made it easy to be certain that only these two had been short-styled when in flower, for all the others had set normal fruits.

In 1889, the part of the field in which these two short-styled plants stood was well cleaned and dug up; nevertheless, towards the end of July of that year I found a group of 12 short-styled individuals nearly in the middle of the field on a spot where not a single *Oenothera* grew in 1886. The new species has since maintained itself on this spot and it has been observed there nearly every year. In the summer of 1894 I saw six plants there in flower; in August of 1898 they were fairly numerous, but since then they have appeared only sporadically.

Before 1895 I thought *O. brevistylis* incapable of setting seed; for I regarded it as being solely male. In 1895 I collected lots of fruits and got a meagre quantity of seed which seemed to me to be empty, so that I did not sow it in the following spring, but when in the following autumn I had gone over my cultures thoroughly I came to the conclusion that it might be worth while to

sow the seed. Of the whole quantity of seed borne by 200 fruits there germinated a little over 300 seeds. That is 1 to 2 seeds per fruit. The mother plants had grown amongst other kinds and were fertilized by humblebees and therefore largely crossed. Nevertheless of the 83 flowering plants to which this seed gave rise 69 or 83 % were *O. brevistylis.*

This result encouraged me to try artificial self-fertilization in parchment bags. For this purpose I chose in 1897 those plants whose stigmas projected farthest out of the tubes; for I had satisfied myself that as a rule these furnished the largest fruits. I harvested seeds from five plants. In 1898 I sowed the seed of each plant separately. Nearly all the young plants flowered between August and October; they were all, without exception, short-styled. Altogether there were 175; some in flower and some only with buds, in which, however, I was able to observe the length of the style.

Oenothera brevistylis, therefore, when self-fertilized, is absolutely constant in spite of its comparative sterility.

B. THE CONSTANT NEW SPECIES.

§ 12. OENOTHERA GIGAS.

(Plate II.)

Oenothera gigas is at once the finest and rarest new species that has arisen in my cultures. Whereas most of the new forms are weaker than the parent species this one is almost in every respect stronger and bigger and more heavily built. A comparison of Plates I and II will show at a glance the nature of the difference between *gigas* and *Lamarckiana*; both represent the top of

the main stem in September, by which time the lower fruits are fully grown. The top of the plant still bears a head of flowers and buds. Figures 60 and 61 represent the same two forms at the beginning of the flowering period.

In warm weather the flowers of the Evening Primroses open in the evening usually at a rate of 2 or 3 a day, seldom more and sometimes fewer according to the weather. They are pollinated by humblebees and by Noctuidae (*Plusia gamma, Agrotis segetum* and others) and as a rule wither during the night. The beauty of the flowers has completely disappeared by the following morning. It is only in cool or even cold weather that the flowers remain open till the following day; but even then they seldom last on into the evening.

The opening of the flowers has been described by E. Roze.[1] The event is a very remarkable one. Early on a beautiful summer evening, when the plants bear nothing but buds and dead flowers, while one may be busied with other operations in the garden, one looks round and suddenly sees every plant in blossom. Half an hour suffices to change the whole aspect of the garden.

The process of opening is in preparation all day. The buds become yellow; their anthers have completely dehisced. The tops of the sepals are still joined together to form an entire cap which however becomes split lower down during the course of the day. The petals gradually swell until at last they veritably burst the calyx open, throw the sepals backwards and unfold their free ends. The whole thing happens in a few minutes or seconds.

[1] E. Roze, *L'épanouissement de la fleur de l'Oenothera suaveolens Desf.* Bull. Soc. bot. France. T. XLII, 8 Nov. 1895, p. 575.

The petals now stand out in the form of a cross; their inner halves being still rolled up together. But it is not

Fig. 60. *Oenothera gigas.* Top of a stem just beginning to flower. A petal has been removed from the flower *a*. *b*, a withering flower.

long before these unfold and set the anthers and the style free.

My new species agree in all these points with the

parent species and its related forms, *O. biennis* and so forth.

One of the most distinctive features of *Oenothera gigas* lies in the breadth of the petals. The swollen

Fig. 61. *Oenothera Lamarckiana.* Top of a stem beginning to flower. *a*, the lowest flower withered and fallen down on the bract.

character of the buds is due to this feature; as also is the cup-like shape of the base of the open flowers. The petals in this species, as in Lamarck's Evening Primrose,

are obcordate and more or less deeply emarginate at their broad apices. In both species the petals are about 3 cm. long; but in *O. Lamarckiana* they are 5 cm. broad, whilst in *O. gigas* they are 6 cm.

I did not find any other differences worth mentioning in the absolute or relative dimensions of the flowers. The size of the flowers of both species gradually decreases as autumn comes on, a fact which must be borne in mind when we are looking for constant differences between the two. The same is true of the calyx tube and of the tip of the calyx, of the height of the stigma and of the anthers and so forth. Speaking broadly *gigas* is more compact than *Lamarckiana*; and though its flowers do not exceed those of its parent species in number, they form a denser and therefore more beautiful head on the stem.

The fruits of *O. gigas* are very different from those of *O Lamarckiana*: they are half as long but about as stout. The seeds are on this account less numerous; but they are larger and heavier.

Oenothera gigas is stronger than the other species in almost every respect. This is seen most strikingly in the girth of the stem as shown in Plates I and II and in figures 60 and 61. The stem is stronger right from its base, and for that reason grows more vertically upwards —a feature which greatly facilitates the recognition of the young plants. In the flowering region the diameter of the stem is almost twice as large as it is in *O. Lamarckiana,* in which it is at most 5-6 mm.: in *gigas* it is often 10 mm.

The whole stem is much more thickly beset with leaves and the leaves themselves are broader, more numerous, and more or less recurved. The great number of leaves is due to the shortness of the internodes; in the

flowering part of the stem I found the length of the internode between two nearly ripe fruits to be barely 0.5 cm. Moreover the leaves are broader, the bracts bigger and, for this reason, the whole fruit-bearing spike less naked.

Fig. 62. Full grown radical leaves in August to show the difference in breadth. L, *Oenothera Lamarckiana*; G, *Oenothera gigas.*

I recognized the species, when I first saw it in my cultures in 1896, by its short stumpy fruits crowded together and also by its cup-shaped flowers.

Although *gigas*-plants can be recognized before they flower it is difficult to give an accurate description of their leaves because they exhibit a high degree of individual variability—much greater in fact than do those of the parent species. The greater breadth is the chief difference; the length and general shape are about the same. The leaves, moreover, of *gigas* are more crumpled (compare page 310 and Fig. 62). But the breadth which is usually a matter of 4-6 cm. sometimes sinks to

Fig. 63. *Oenothera gigas.* A young plant in June, a few days before transplanting, (1/2).

2 cm. without however destroying the characteristic look of the species. The leaves of the stem are usually set on a shorter stalk and are more deeply toothed than in *O. Lamarckiana.* The branches, of which a great many develop, remain sessile in the axils of the leaves as short densely foliate spikes which tend to make the foliage on the stem much thicker, just as in *O. oblonga* (Fig. 71).

The difference between the young rosettes in June (when they are usually planted out) is very striking.

The cotyledons are at that time still present; but dying off; or perhaps already dead. Figures 63 and 64 represent two plants at this age reduced to the same scale (½). The *gigas* rosettes are compact, round and stout; the *Lamarckianas* are looser, their leaves have longer petioles

Fig. 64. *Oenothera Lamarckiana.* A young plant in June, a few days before transplanting (½); *c*, the cotyledonary leaves.

and therefore make less use of the space of ground at their disposal.[1]

Oenothera gigas has only appeared once in my cultures—a single specimen in 1895. The event has already

[1] Miss Anne M. Lutz discovered another highly interesting difference between *O. Lamarckiana* and *O. gigas* The former has 14 chromosomes in its nuclei, like *O. biennis* and other species, but the nuclei of *O. gigas* have twice as many, viz., 28. Cf. *Science,* Vol. 26, Aug. 2, 1907, p. 151., (Note of 1908.)

been described in § 3 (p. 227). It was evident that it was a constant species directly its seeds germinated. As

Fig. 65. Seedlings of *Oenothera Lamarckiana* (*L*) and *O. gigas* (*G*). *c*, the cotyledons. Magnified; the natural size shown in the middle.

soon as they have acquired their first and second leaves the seedlings can be distinguished from those of the parent species with perfect ease (Figure 65). Their leaves are not only broader but more or less markedly cordate at their base. The latter character is gradually lost in the succeeding leaves but the broader base persists for some time longer as a convenient mark of identification (Fig. 66).

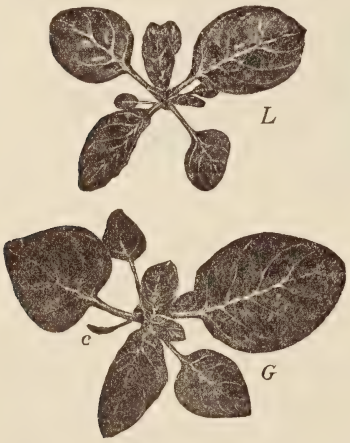


Fig. 66. Older seedlings of *O. Lamarckiana* (*L*) and *O. gigas* (*G*). *c*, cotyledons, red. to $^2/_3$.

This character made it possible for me to demonstrate the constancy of the new species in the second, third and fourth generations (1897, 1899, 1900) without having to grow more than 20 to 40 plants to maturity.

O. gigas has appeared twice again, but not directly from *O. Lamarckiana.* It appeared once in 1898 from the seeds of a plant of *O. sublinearis* which had itself arisen from the *Lamarckiana*-family. It appeared again in 1899 from a cross made between *O. lata* and *O. hirtella,* a new species which did not arise from my mutating families but turned up among the seeds which I had bought.

I succeeded in getting the first of these *gigas*-plants to flower, but it was annual and did not flower till the beginning of October, too late for the seed to ripen. I therefore compared the plant very carefully with the other plants of that species which I had growing at that time, and which were raised from *gigas*-seeds; it agreed with them in all essentials.

The plant which mutated from *O. lata* died as a rosette and never developed a stem.

§ 13. OENOTHERA RUBRINERVIS.

This form unlike *Oenothera gigas,* is one of the commonest of my new species. It has arisen, altogether, 66 times from *O. Lamarckiana* or from other families or cultures. It is hardly necessary to state that among the ancestors of these mutants, as far as I have had them under observation, there have been no examples of *rubrinervis.* And, as the genealogical tables given above show, most of the mutations arose in families which had been under observation for many generations.

The 66 mutated plants belonged to a single type. They did not differ more from each other than the members of a culture raised from the seeds of a single one of them. Each of the characters, which have al-

ready been briefly described on p. 230 and will be treated of in detail shortly, was present on every individual plant; and, as far as investigated, the characters did not differ from plant to plant.

Once the young rosette is recognized its future peculiarities can be predicted, as in the example of the mutation of which Fig. 48 is a photograph, which was also photographed again when it was in flower (Fig. 49) (See pp. 280 and 282). I have often planted the mutants singly or in groups so soon as I have recognized them in order to be able to follow their further development during the course of the summer.

It is very important to note that the various characters, the red coloring, the brittleness, the narrow leaves, the hairy appearance, and so forth, have never appeared separately. It is obviously out of the question that this association can be ascribed to chance, seeing that it has occurred in 66 cases. There can be no doubt that there is some sort of a connection between them.

This conclusion receives strong support from the fact that even in the offspring of crosses the *rubrinervis* characters remain associated, as I have observed in numerous cases. And exactly the same is true not only of the newly arisen mutations but of the offspring of crosses made with them. Every species has its "type" according to which its whole nature is altered; this "type" affects its whole organization in such a way that hardly a character or an organ is untouched by it.

This hidden connection between characters which are invariably associated together needs an explanation. Two possibilities present themselves. First, it is conceivable that all these visible characters are only expressions of a single change, and that a mutation is brought about by

the appearance of a single new elementary character. On the other hand it might be supposed that in mutation the elements of the species are changed by groups. There

Fig. 67. *Oenothera rubrinervis.* An entire flowering plant, 1900. Fourth generation of a *rubrinervis*-family which arose in 1895 from seeds of *O. Lamarckiana* as shown in the pedigree on page 262, that is to say from the second generation of *Lamarckiana* in that culture.

is abundant *a priori* and *a posteriori* evidence for the view that the characters of plants are often associated in groups in such a way that whole series of them react

as one unit to external stimuli, and also that in hybridization and other breeding experiments these characters behave as if combined into inseparable groups.[1]

If we should ultimately succeed in splitting up the group of *rubrinervis*-characters into its component units we should of course demonstrate its compound nature. But until this has been done it seems to me both simpler, and better in accord with the facts, to adopt the view that the sum total of the characters is the expression of a single elementary "unit."

How it comes about that this "unit" can make the walls of the bast-fibres thin, the leaves narrow and gray-green, the veins and fruits reddish, is a question which cannot be answered at present. But chemical combinations also possess many attributes the interdependence of which one is far from being always able to explain.

I shall not go further into this question now; but before I leave it I wish to insist on the fact that the whole so-called "habit" of a species can be so much altered by a mutation that, during its whole life and in every organ it differs from the species from which it arose.

If we refer to the pedigrees and tables of mutations given in sections 1-8 we shall find the cases of *O. rubrinervis* which are recorded in the following table. In it we see that one *O. rubrinervis* occurs in about every 1000 seedlings.

Besides this, *O. rubrinervis* arose twelve times in other cultures which were either lateral branches of the pedigrees referred to, or had arisen from crosses. I have summarized these in Table II.

The proportion of *O. rubrinervis* to the whole num-

[1] *Intracellulare Pangenesis,* pp. 21, 33, ec.

ber of seedlings will be seen to be much greater than in the first table. It amounts here to about 6 per thousand. But it must be mentioned that only those cases are in-

INDIVIDUALS OF OENOTHERA RUBRINERVIS WHICH HAVE ARISEN BY MUTATION.

I

SOURCE	YEAR	SEEDLINGS TOTAL	SEEDLINGS RUBRINERVIS
O. Lamarckiana	1890, 1895 / 1896, 1897	33,800	32
A branch of the same family	1895, 1896	10,000	9
O. laevifolia	1889, 1894	—	4
O. lata	1900	2,000	3
O, oblonga	1897	45	1
O. Lamarckiana × *O. nanella*	1897	1,051	2
O. lata × *O. nanella* . . .	1895, 1900	222	2
O. Lamarckiana from the field	1889	—	1
		Total	54

INDIVIDUALS OF OENOTHERA RUBRINERVIS WHICH HAVE ARISEN BY MUTATION.

II

SOURCE	YEAR	SEEDLINGS TOTAL	SEEDLINGS RUBRINERVIS
O. Lamarckiana, a biennial culture	1897	164	2
O. lata which mutated from *O. Lam.*, first generation . . .	1896	326	4
O. lata × *O. Lamarckiana* . .	1898, 1900	750	2
O. lata × *O. brevistylis* . . .	1896	266	1
O. nanella × *O. brevistylis* . .	1895	270	1
O. scintillans × *O. nanella* . .	1898	95	1
O. Lamarckiana arisen from the cross *O. Lam.* × *O. scintillans*	1900	80	1
	Total	1951	12

cluded in which the species in question actually occurred and that a figure which properly represents the proportion of *O. rubrinervis* cannot be obtained without including

all the cultures irrespective of whether they contained it or not. On the latter estimate the number would probably sink to 0.1 %, if not lower.

It has already been stated that *O. rubrinervis* can be recognized as quite a young plant. Pans or boxes containing nothing but *O. rubrinervis* can be identified very

Fig. 68. Seedlings of *Oenothera rubrinervis* at various ages; *c*, the cotyledons; *A*, with the first two leaves at the beginning of May; *A'*, the natural size of the same. *B*, 14 days older. *C*, Rosette, towards the end of June, just before transplanting, from a pan in which the seedlings were growing very close. Compare Fig. 64, p. 325 and Figs. 65 and 66, p. 326.

early, a good deal earlier than mutants standing amongst other species (Fig. 48 on page 280). But in these the narrow leaves with their red veins and gray felt-like surface, the almost complete absence of crumples and the brittleness especially of the stalk, clearly distinguish this form from *O. Lamarckiana* and the rest. (Compare

Fig. 68 with the similar ones of *O. Lamarckiana* Figs. 64-66).

The narrow form of the leaves is well brought out in Figs. 52 and 54. The older the plants become the greater becomes the difference and the more certain the diagnosis. As a rule I have removed the mutants at an age when they have about twice as many leaves as the rosette figured at Fig. 68 C. The plants shown there are, of course, not mutants but are raised from seeds of *O. rubrinervis* and selected from the crop as the most typical examples of that species.

As the plants get older the veins of the leaves lose their pale red color more or less; but this depends on how they are grown and on the amount of sun they get. On the other hand, with age the red pigment becomes more evident in the inflorescences, the flowers and the unripe fruits, thereby contributing greatly to the characteristic look of the species. The young internodes of the stem are suffused with red, and this color is particularly pronounced in the swollen bases of the larger hairs. The tips of the calyx are spotted with red and the flowers become much darker when they wither than those of *O. Lamarckiana,* reminding one of those species the leaves of which become red when they wither, such as *O. stricta, O. missouriensis,* and particularly the white *O. acaulis.* The fruits are marked with four broad, dark red, longitudinal stripes, one along the middle of each valve. But in this case the redness varies according to the position of the fruits and from individual to individual within apparently wide limits; sometimes, indeed, the stripes are very difficult to find.

This red pigment occurs also in *O. Lamarckiana* and particularly in the unripe fruits; but very indistinctly:

whilst in *O. rubrinervis* the red stripes are handsome and striking.

To turn now to the general structure of the plant; it has a greater tendency to develop lateral branches from the main stem and, in connection with this fact doubtless, fewer from the rosette (compare Figs. 49 and 67 with Fig. 55). But this feature is greatly affected by the manner of cultivation.

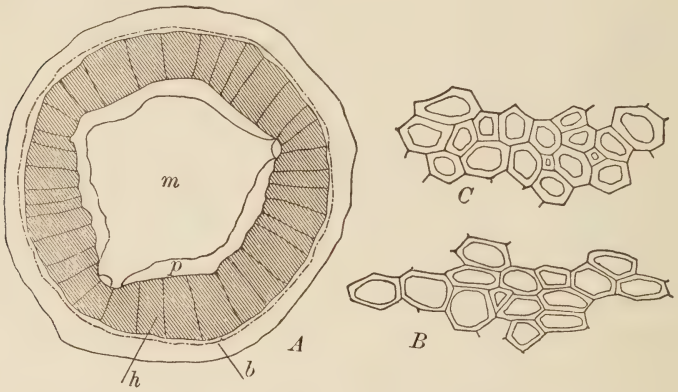


Fig. 69. *Oenothera rubrinervis. A,* Transverse section of the stem; *m.* pith; *p,* inner phloem; *h,* wood; *b,* bast bundles between the outer phloem and the bark; *B,* part of such a bundle highly magnified; *C,* the same of *O. Lamarckiana.*

This form can be distinguished at some little distance, from the common Evening Primrose by the general habit of its inflorescence and flowers; but it is very difficult to find differentiating characters which can be described. Plate I might, if it did not lack red pigment, pass as well for a *rubrinervis* as a *Lamarckiana* (see Fig. 43, p. 232).

The whitish gray color, which is seen in a more pronounced state in *O. albida,* is not really due, as it appears to be, to the greater hairiness of the plant; but is brought about by the swollen surfaces of the cells of the epidermis

which have not grown out in the form of hairs. This swelling is very slight in *O. Lamarckiana.*

It has already been stated in § 3 of this Part that one of the most characteristic features of *O. rubrinervis* is the brittleness of its stem. The latter as well as the petioles of the leaves are very fragile and break off at the merest touch. The cause of this is the weak development of the hard bast. It is only biennial plants or very strong annual ones that break in late autumn in the way that *O. Lamarckiana* does when the hard bast is torn.

A transverse section[1] of the stem of a plant about a meter high, taken in August, shows the bast-fibres in a discontinuous ring around the outer side of the wood and inside the bark, as shown in Fig. 69 *A*. If we compare such a section with a similar one of *O. Lamarckiana* we do not at first see any difference. In both plants the sclerenchymatous strands are about equally developed. But if we examine a single strand under a higher power we find that in *O. Lamarckiana* it is better developed in the radial and less so in the tangential direction than in *O. rubrinervis.* The most important difference however lies in the thickness of the walls of the individual cells which, as Figs. 69 *B* and *C* show, are about half as thick in *O. rubrinervis* as they are in the parent species.

There is great difference between individuals in respect to this character depending on whether they have plenty of room to grow in, or are crowded together; or whether they are sown early or late. Weak plants never entirely lack the bundles, though the individual cells of the bundles are fewer and more tangentially arranged. They often retain these characters until they ripen their fruits.

[1] For the general anatomy of the stem see Francis Ramsay, *On the Stem Anatomy of Certain Onagraceae,* Minnesota Botanical Studies, Bull. No. 9, Nov. 1896, p. 674.

In late autumn there appears on the inner side of the sclerenchym ring a thin layer of cork which must of course have been laid down much earlier and possibly stands in some causal relation to the external characters of the plant.

Fig. 70. *Oenothera rubrinervis.*— Young annual plant, 30 cm. high, about $^1/_3$ natural size. To show the zigzag course of the brittle stem.

This species is characterized by an apparent inability to stretch its stem — so to speak — which is particularly noticeable in weak plants. This character is, in all probability, due to the weakness of the bast-fibres we have just described. Fig. 70 represents a young plant grown in a pot, about the beginning of July, and illustrates this feature very well. The stem is not straight but bent in a zig-zag fashion; in such a way that the bends occur at the nodes and the leaves are inserted in their outer convex sides. These bends do not straighten out with subsequent growth; in fact they are often even more pronounced on the fruiting plants. The stronger the stem is, the less is this character developed; but I have,

nevertheless, found it on perfectly healthy annual plants whose main stems have been heavily laden with fruit.

I have already recorded experiments on the constancy of *O. rubrinervis* § 3 (p. 232) and § 5 (p. 274). These experiments show that plants raised from the seed of mutated individuals are exactly like their parents, and that the characters we have described for the parents reappear in the children in exactly the same degree. *O. rubrinervis* itself is very slightly mutable and seems to confine itself to throwing off *lata* and *leptocarpa,* as already shown on page 273.

§ 14. OENOTHERA OBLONGA.

(Plate VI.)

O. oblonga has arisen much more frequently than *O. rubrinervis* both from *O. Lamarckiana* itself and other species and crosses. I have seen it arise altogether about 700 times from one form or another of known and pure ancestry. The various cultures in which it arose comprised about 70,000 seedlings. We might therefore almost speak of coefficients of mutation; which in the case of this species would be about 1 %, in the case of *O. rubrinervis* 0.1 % and in that of *O. gigas* 0.01 %.

What is the cause of these differences? They cannot be ascribed to defective observation. I first saw *O. oblonga* in 1895 when my cultures were very extensive; in previous years they were probably there, but escaped my observation. Their young rosettes are as easy to recognize as those of *O. rubrinervis*; and often somewhat earlier, as rosettes with six leaves. But evidently this

fact cannot explain the difference in the mutation-coefficients.

Fig. 71. *Oenothera oblonga.* Upper and middle section of a plant in September to show the peculiar type of branching with rosette-like lateral branches. (Compare Fig. 67 on page 329.) Reduced to $^1/_3$ natural size. The smaller figures similarly reduced. *a*, a flower; a petal is removed and shown separately at *b*; *c*, a flower without the corolla, showing the stamens which are bent downwards at the base but upwards again towards their tips, and the style with the four stigmata; *d*, ripe fruits; *e*, one of their bracts.

These differences in the "mutation coefficients" hold good, too, of the individual families. Not exactly of course, but to such an extent that in large sowings the

oblonga mutants are almost always considerably more numerous than the *rubrinervis* ones. The observations extend over six years (1895-1900), which is probably only a small section of the whole mutation period. Nevertheless, the evidence seems to justify the conclusion that the various new species arise from the parent form, at any rate for a certain period, in definite and constant proportions which vary from species to species.

This consideration seems to me to lead to two important points. First, the probability that *O. Lamarckiana* is able to produce other mutations in even smaller proportions, such as one in a million; in which case there would not be much chance of their appearing in my cultures. In other words if one could make the whole experiment ten or a hundred times as extensive, one would be very likely to get more mutations and amongst them, possibly, some better than those which have already appeared. *O. laevifolia* and *O. brevistylis* might then arise again.

The second point relates to the causes of these proportions. Is it possible to interfere with and alter the "mutation coefficients"? Is there any hope of increasing the proportion of the rarer species?[1] And when a method of doing this will be invented will it be possible to obtain mutations which are at present presumably too rare to appear?

An experimental study of the process of mutation during the mutation period may even put into our hands the power to bring about the inception of such a period; or in other words the power to make an immutable species mutable.

[1] See the case in § 5 (on page 264) where, as a result of defective germination the proportion of mutants arose to 40 %.

But let us return to the figures which seem to justify these hopes.

I shall first give the values for the chief families and then those for their lateral branches.

INDIVIDUALS OF OENOTHERA OBLONGA WHICH HAVE ARISEN BY MUTATION.

I

	DATE	SEEDLINGS TOTAL	SEEDLINGS OBLONGA	% OBLONGA
		A. FROM O. LAMARCKIANA.		
Main family . . .	1895	14,000	176	1.3
" " . . .	1896	8,000	135	1.7
A collateral family	1895	10,000	69	0.7
Biennial culture .	1897	1,660	31	1.9
	Totals	33,660	411	1.2
		B. FROM O. LATA.		
Lata-family . . .	1900	2,000	7	0.3
Lata-cultures .	1895–1898	2,350	28	1.2
	Totals	4,350	35	0.8
		C. FROM O. NANELLA.		
O. nanella . . .	1897	760	1	0.1

Although the *lata*-family of 1900 is considerably below the average, the percentages in groups A and B conform pretty closely to a general proportion of about 1 %; whilst the figure for *O. nanella* affords a good example of the rule that new species mutate less than *O. Lamarckiana* or than *O. lata* fertilized with *Lamarckiana* pollen.

About the same proportion is maintained in crosses. The following table embodies results already described, together with some to be referred to later on.

INDIVIDUALS OF OENOTHERA OBLONGA WHICH HAVE ARISEN BY MUTATION.

II

FROM CROSSES.

SOURCE	DATE	SEEDLINGS TOTAL	SEEDLINGS OBLONGA
O. Lamarckiana × *O nanella* .	1897–1899	8283	38
O. Lamarckiana × *O. brevistylis*	1898	293	4
O. lata × *O. nanella*	1895–1900	1586	14
O. lata × *O. brevistylis* . . .	1895–1899	498	6
O. lata × *O. laevifolia* . . .	1895	127	4
O. rubrinervis × *O. nanella* .	1895	1500	4
O. scintillans × *O. nanella* . .	1898	95	3
O. Lamarckiana × *O. biennis* .	1896	30	2
O. Lamarckiana × *O. suaveolens*	1897	200	8
	Totals	12,612	83 = 0.7 %

To obtain the above figures I have sometimes recorded the seedlings when they had from 6 to 8 leaves but at other times later, according to the different years and various other circumstances. In many cases I have transplanted them in order to observe them during the whole summer. Fig. 72 gives an idea of the stage at which the seedlings were recorded, and may be compared with the parallel figures for the *lata*-families (Plate IV and Fig. 48, p. 280). We are concerned in Fig. 72 with a culture of *O. Lamarckiana* which was sown on the 14th of March 1900 and transplanted into wooden boxes on the 14th of April. The seeds had been harvested in 1895 from three plants enclosed in parchment bags to insure pure self-fertilization. Of the 188 seedlings raised, 4 were mutations of which two were *albida* and two *oblonga*. By a lucky chance an example of each of the new forms stood quite close together; so that I was able to include them in the same photograph (Fig. 72). The

plants are arranged in rows in the boxes: *O. albida* can be recognized at once in the middle of the figure by its small size; just underneath it is the *O. oblonga* which can hardly be distinguished in the figure. I transplanted these two plants on to a separate bed to watch their further development. They grew up to strong rosettes which exhibited all the characters of the species to which they

Fig. 72. A mutation in a culture of *O. Lamarckiana.* Origin of *O. albida* and *O. oblonga.* From a photograph taken at the end of May 1900. In the middle of the middle row is the little *O. albida*; in the middle of the lower row *O. oblonga.* The other seedlings are *O. Lamarckiana*; $^2/_3$ natural size.

belonged, clearly and beautifully; but were destroyed in the autumn by the caterpillars of *Agrotis segetum.*

Seedlings of even less than 6 or 8 leaves can often be recognized; but it is very difficult to describe the characters which render their identification possible. In Fig. 73 at *A* a very young seedling is shown with its

first two leaves, and at *B* a rosette two months old. These are not mutants but plants grown from the seed of self-fertilized *oblonga*. These cultures came quite true to seed and exhibited a high degree of uniformity. The first two leaves, after the cotyledonary ones, are broad and with broad bases, markedly broader than those of *O. Lamarckiana* at the corresponding age (Fig. 65 *L*, p. 326). This can be seen in Fig. 73 *A* and *B* at 1 and 2 as well as in Fig. 72. There soon follow narrower leaves but the rate at which this decrease in breadth takes place is not constant. Fig. 73 *B* is more typical in this respect than the *O. oblonga* of Fig. 72, but the remaining seedlings

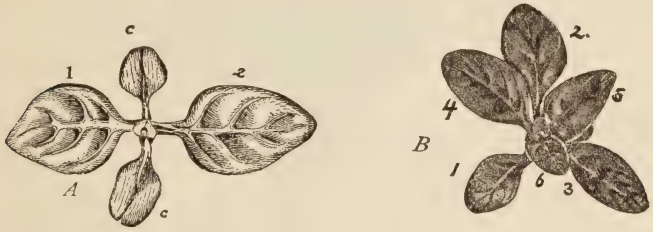


Fig. 73. Seedlings of *Oenothera oblonga*. *A*, a few weeks old, magnified (2.5/1). *B*, two months old, $^2/_3$ natural size. *c*, cotyledonary leaves. In *B* the leaves are marked in the order in which they appeared.

in the same box behaved essentially in the same manner. I photographed many of them at the time, but do not think it worth while to reproduce the others as well.

As the plants grow their characters become more pronounced, the leaves longer and narrower, the veins broader, paler and more prominent. In the third month growth takes place much faster, or at any rate produces a more noticeable increase than in the first two. At the end of that period the rosettes possess many leaves and are very strong and ready for the development of the stem (Fig. 74). If they do not do this they grow to a

considerably greater size during the summer and increase the number of their leaves without, however, altering their general appearance. A very typical leaf with its venation will be found in Fig. 54 (See p. 295).

If the rosettes develop stems in June and July they flower that summer. Such plants are very uniform in character, they are slender and yet firm, and branched either very little or not at all. Hardly any differences were discernible between 200 flowering plants growing

Fig. 74. *Oenothera oblonga.* A rosette with radical leaves at the end of June.

together. The tallest plant began to flower when it was 60 cm. high, and flowered till the end of September when it had attained a height of one meter. It had a single lateral branch only 10 cm. long and with only two flowers on it; all that there was in the way of lateral branches besides this was a series of rosette-like offshoots from the axils of the leaves along the middle region of the stem. The result of this is the very characteristic *ensemble*

(Fig. 71 *B*) which is always found in all the plants of this species. The culture in question did not contain a single plant bearing flowers on a lateral stem, with the exception of the plant referred to.

At the time when the plant is about to flower (Fig. 44, p. 233) the flowering spike is still densely clothed with leaves. Higher up, the bracts become shorter. The fruits likewise do not attain the size of those of *O. Lamarckiana*; and we get in this way another very striking character which can be well seen by comparing Plate VI with Plate I. The ripe fruits hardly attain a third of the length of those of *O. Lamarckiana.* As a result of this, the seeds are often bad and developed in very small quantity so that all that can be hoped for is a very meagre harvest at the best.

Biennial plants are much better in this respect; they are more robust and bear numerous, strong, though small, fruits which contain an abundance of seed. These fruits are not much longer than those of the annual plants but much stouter, rather like those of *O. lata.*

When grown under more favorable conditions the annual as well as the biennial plants develop a certain number of lateral stems from the axils of the radical leaves, such as have already been figured in the case of a mutation from the *lata*-family (Fig. 50, p. 284). But, even so, the main stem itself remains unbranched, a peculiarity which can best be seen by comparing such a plant with *O. rubrinervis* (Fig. 49, p. 282).

There is not much to be said about the flowers and buds of *O. oblonga* (See Plate VI). They have the same form as those of the parent species; but in correspondence with the greater delicacy of the whole plant they are a trifle smaller.

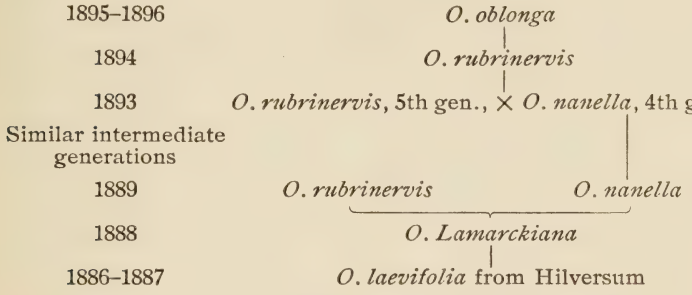
I first harvested the seed of *O. oblonga* in 1895; but as the plants had flowered too late they had not been artificially fertilized and the seed only gave quite a small percentage of *oblonga*. But in 1896 I harvested self-fertilized seed partly from annual and partly from biennial plants. The plants were all mutants, that is, had all arisen from *O. Lamarckiana* of pure strain, in fact from the main line of descent of the *Lamarckiana*-family itself (See the genealogical table on p. 224). The biennial plants had therefore three generations of pure *Lamarckiana* behind them; and the annual ones four. There were seven plants in the first and twelve in the second group.

I sowed the seed in the middle of April 1897, and as the seed had not been sown too thick the seedlings displayed their characteristic features as early as the middle of June, in the seed pans. The leaves with the exception of the first two broad ones (p. 342) were narrow and had long petioles; and exhibited the characteristic broad pale midveins. A comparison with cultures of the ordinary Evening Primrose at the same stage of development made it certain at once that there were no *Lamarckianas* among the *oblonga* crops. The sowings were perfectly true, with the exception of four seedlings one of which became a *rubrinervis*, one an *elliptica* and two *albida* (p. 297). Besides this, one plant had a pitcher shaped leaf. I counted the seedlings for 17 out of the 19 seed parents separately; and, as I have already stated above (p. 235), they were all, with the exceptions named, *oblongas* (1683 and 64; together, 1747 plants).

In the same year I sowed the self-fertilized seed of three other mutants which had arisen, in order to find out whether the difference in their origin would cause

them to differ from the other mutants in the matter of constancy. I will describe the ancestry of the three plants separately.

The first arose from the *laevifolia*-family, whose pedigree has been given on p. 273, in the following way:



The first three generations in this pedigree as well as the *rubrinervis* of 1893 have already been referred to on p. 273. The *O. nanella* was biennial in 1889, but since then has been annual. In the summer of 1893 I pollinated some castrated flowers of *O. rubrinervis* with the pollen of *O. nanella*; in 1894 I obtained from these seeds some ordinary *rubrinervis* plants, which were fertilized with their own pollen and produced mainly *O. rubrinervis*. But amongst them were four *oblonga* (p. 341) of which I managed to bring one safely through the winter as a rosette. It flowered in 1896 in a parchment bag; 16 seedlings were raised from it and were subsequently transplanted into pots; they were all *oblonga*.

The second *oblonga*-mutant arose likewise from the *laevifolia*-family. It arose from a self-fertilized *Lamarckiana* plant, in the main line of descent in 1894, a plant which had itself therefore arisen partly from *laevifolia* and partly from *Lamarckiana* stock, but which, at

least so far back as 1896, had ancestors of no other type. This *oblonga* belonged to the 9th generation of the family. It was biennial; was self-fertilized and gave rise to 297 seedlings. Amongst these I found a single *O. albida*; all the rest were *O. oblonga.*

The third plant belonged to a lateral branch of the *Lamarckiana*-family. In the pedigree on p. 224 five *lata* plants will be found for 1888. One of them which had a fine ascidia flowered in 1889; but its seeds were not sown till 1894. This second generation was annual and left to be pollinated by insects. In 1895 I raised from its seeds 128 *Lamarckiana,* 18 *lata,* 3 *nanella* and 10 *oblonga.* Of the latter one plant flowered in its second year, i. e., in 1896, in a parchment bag. Of its seeds 91 germinated and gave rise solely to *oblonga* plants.

These experiments show that the constancy of *O. oblonga,* when it arises as a mutant, is independent of the character of its ancestors. These may be *Lamarckiana, lacvifolia, rubrinervis, nanella,* pure or hybrid, but the *oblonga* which arises from them is always pure from the first generation; except, of course, that it has inherited the mutability of its parent and has the capacity for giving rise to other types (*albida, rubrinervis*).

The total number of plants recorded in the experiments of this year is $1747 + 16 + 297 + 91 = 2151$. I have sown seeds of the same mother plants in subsequent years, in 1899 and 1900 and always with the same result. I have so far not harvested any seed of the second generation because although the plants flowered freely they were all annual and so produced only imperfect fruits.

§ 15. OENOTHERA ALBIDA.

(Plates III and IV.)

A beautiful but delicate species which is very slow in growing as a seedling and is for that reason very easily recognized. See Fig. 48 on p. 280 and Fig. 72 on p. 342. These weak plants are at a great disadvantage when growing among the much stronger seedlings of the parent type; and it is only very rarely that I succeeded in getting them to flower.

It was in 1895 (as has already been stated in § 3, p. 229) that I first succeeded in getting a rosette to sur-

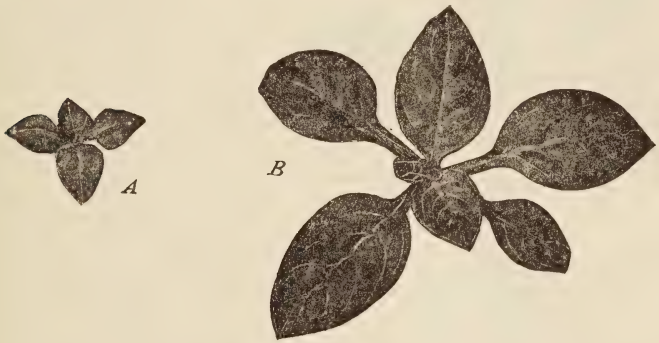


Fig. 75. *Oenothera albida.* Young seedlings; *A*, with the first two leaves; *B*, two months old.

vive the winter; it was on it that I first saw the flowers of the new species, but I got no seed from it. Before this I had seen *albida* almost every year and in no inconsiderable numbers, but thought they were merely sickly individuals and had taken no further account of them. That is why the records that follow are confined to the period 1895-1900.

The young *albida* plants are so delicate that it is only by the exercise of the greatest care that they can be kept

alive. I never found them at Hilversum; and even if they had ever succeeded in germinating there, they would most certainly have perished before developing a stem. This was exactly what happened in my experimental garden from the time my experiments began until 1896. These facts moreover show, as mentioned above (p. 229), that my first *albida* mutants could not have had similar individuals in their ancestry, neither as pollen parents nor as seed parents.

Fig. 76. *Oenothera albida.* Young plant, $3^1/_2$ months old.

Even when *O. albida* has set seed the difficulty of getting the seed to germinate is considerable; but the attempt to keep the young plants strong from the very beginning has succeeded. Some of them always remain weak and look just like the young mutants, others bear broader leaves and gradually grow to little rosettes which are apparently just as strong as those of *O. oblonga* at a like age (see Fig. 75). Moreover they differ from these very little in form at first (Fig. 73). But their color is always, as their name implies, a whitish gray. For the first six weeks of their existence the leaves of these two species are about the same breadth; those of *O. albida* however are a little blunter at the

tip. During the growth the leaves of the rosettes increase in breadth as a rule (Fig. 76) whilst those of the stem become narrow again (Fig. 54 *a* on page 295).

It is always easy to recognize *albida* mutants by the characters I have described. I have cultivated many of them beyond this stage, especially in 1895 and the following years, in the hope of getting them to flower and set seed. And in this way I had ample opportunity of testing the accuracy of my diagnosis.

The ease with which this species can be recognized as quite a young plant makes it a convenient one for the study of the relative frequency of its origin from *O. Lamarckiana* and other species. The result of this investigation was that this frequency, this coefficient of mutation, turned out to be very different in different cases and to be subject to even greater fluctuations than those exhibited by the three species described above (0.01 % for *O. gigas,* 0.1 % for *rubrinervis* and 1 % for *oblonga*).

The two tables that follow bring this out. I include in them figures that have already been given in §§ 2-5.

INDIVIDUALS OF OENOTHERA ALBIDA WHICH HAVE ARISEN BY MUTATION.

I

SOURCE	DATE	TOTAL	SEEDLINGS ALBIDA	SEEDLINGS % ALBIDA
O. Lamarckiana-family .	1895–1899	28,500	56	0.2
O. Lamarckiana, plants from crosses	1898	4,599	2	0.05
A lateral branch of the *Lamarckiana*-family .	1895	10,000	255	2.5
O. lata	1900	2,000	42	2.1
O. lata	1896–1899	751	31	4.0
O. Lamarckiana, biennial	1896	164	15	9.0

The proportion of *albida* mutants varies between 0.05 % and 9 %.

This variability is also exhibited though to a considerably less extent by the proportions in which *O. albida* occurs among the offspring of various crosses.

INDIVIDUALS OF OENOTHERA ALBIDA WHICH HAVE ARISEN BY MUTATION.

II

FROM CROSSES.

CROSS	DATE	TOTAL	O. ALBIDA	% ALBIDA
O. Lamarckiana × *O. nanella*	1897	1341	1	0.1
O. lata × *O. nanella* . .	1895–1900	1586	15	1.0
O. lata × *O. rubrinervis* . .	1900	1844	37	2.0
O. lata × *O. scintillans* . .	1900	636	2	0.3
O. scintillans × *O. nanella* .	1898	95	3	3.0
O. lata × *O. suaveolens* . .	1900	743	13	2.0

The mutants obtained in these two series of experiments amounted to 472 and agreed in all their characters so far as these could be investigated.

Flowering plants of *O. albida* can be distinguished from all other subspecies of *O. Lamarckiana* and from this species itself just as easily as the seedlings and rosettes can. They do not attain even in late autumn a height of more than one meter; but as a rule they give rise, about the middle of their stem to a group of flowering branches, in the same way that *O. rubrinervis* does. Their leaves are narrow (Fig. 54 *A*, p. 295), pointed and very uneven; the crumples in them being more numerous and more pronounced than in the parent species (Fig. 57, transverse section of a leaf, see p. 310).

The flowers are always somewhat smaller than those of *Lamarckiana*, as would be expected from a greater delicacy of the species; moreover they have a tendency

to stand more upright, and not to open so wide as those of the parent species (compare Plate III with Plate I). In other respects they have the same structure, and the stigmas stand up well above the anthers. The color of the flower is a paler shade of yellow. The fruits do not attain the length or the stoutness of those of *O. Lamarckiana,* and as a rule set little seed.

The gray color, which, like that of *O. rubrinervis* is not due to increased hirsuteness, but to the swelling of the outer wall of the ordinary epidermis cells, exhibits a high degree of individual variability, sometimes indeed to such an extent that doubt may arise as to the proper diagnosis, a doubt which however can always be dispelled by the examination of later stages.

§ 16. OENOTHERA LEPTOCARPA.

The foregoing examples have shown us that mutations arise from *Oenothera Lamarckiana* in proportions which vary from about 1 % to less than 0.1 %. We have further seen that the same mutations recur regularly in the same mutation period.

It follows from this that a careful study of such a period will soon reveal the commoner mutants which the species in question is producing. Then we have to look for the rarer ones; and for this purpose much more extensive sowings must be made.

If these rare mutations can be recognized as seedlings or at any rate as young rosettes, all that we have to do is to sow seed on a large scale, transplant any seedlings which exhibit any abnormality and throw away those which have not mutated. If this method is adopted

many thousands of plants can be accommodated on a few square meters of ground up till the time when the mutants have to be planted out.

But if the characters do not develop whilst the plant is young, it is a very different matter indeed. In this case 40 to 50 is the maximum number of plants that can flower on a square meter, and that is a high estimate.

When this is the case the plants must be cultivated on an enormously extensive scale before we can entertain the smallest hope of seeing mutations. We become dependent to a large extent on chance as in the case of the first appearance of *O. gigas*.

It is obviously for reasons of this kind that practically all my mutations are recognizable as seedlings, whilst the two new species which are found at Hilversum are indistinguishable in their young stages from young *O. Lamarckiana*.

Oenothera leptocarpa is the only exception to this rule, at least it is the only one among those which have arisen from the pure stock of *O. Lamarckiana*. Amongst the crops raised from crossed seeds there were occasional instances; but it is often difficult in these cases to distinguish mutations from the ordinary products of crossing.

O. leptocarpa cannot, even in pure cultures, be distinguished from *O. Lamarckiana* either as a seedling or as a rosette or even at the period when it is first developing its stem. I have once or twice transplanted supposed mutations as young plants and found them to be *O. leptocarpa*. But as a rule I have not recognized them until just before they flowered.

For these reasons little can be said with certainty about the frequency with which this form appears. The

origin of two examples of this species will be found recorded in the pedigree of a branch of the *Lamarckiana*-family which appears on page 262. It occurred in a culture of about 10,000 seedlings in 1895, of which about a thousand flowered. This indicates a frequency of about 0.2 %. I have noted the appearance of single individuals both before and after this, but have not the data from which to calculate the frequency of their occurrence.

O. leptocarpa has arisen from *O. rubrinervis,* as well as from *O. Lamarckiana,* but not from any other new species. After I had become familiar with this fact I found them fairly frequently. A character peculiar to *O. leptocarpa* is that it flowers very late—a character which has greatly diminished the prospect of discovering the species. For as soon as the plants on a bed begin to flower, seed-parents are chosen for self-fertilization. And I generally remove a certain number of the plants surrounding these either to allow them to grow more freely or to have plenty of room for my operations. This involves the destruction of the weaker plants with which the late flowering *leptocarpa* are easily confused.

The *rubrinervis* cultures were usually made with a rather special end in view and therefore consisted of no more plants than were wanted as seed parents. The plants were grown for example for the purpose of making certain crosses which I had decided upon or for the experiments with tricotyly which I have already mentioned, and in these latter of course selection took place directly the seed came up. So that the proportion in which *leptocarpa* appears in such cultures is no indication at all of what the mutation-coefficient of that species really is.

For example in 1895 I found 5 *leptocarpa* amongst 44 tricotylous *rubrinervis* (p. 273) and in 1897 I found one amongst 20. In 1900 I had planted out 24 apparent *Lamarckiana* plants which had sprung from a cross which I had made in 1899 between *O. rubrinervis* and *O. nanella.* When they came to flower, however, it turned out that only half of them were really *Lamarckiana* and that the rest were *leptocarpa.* In the same year two *leptocarpa* appeared among the 90 offspring of a cross between *O. rubrinervis* and *O. Lamarckiana.*

The most characteristic features of *O. leptocarpa* are its late flowering and its long slender fruits. The late flowering is not the result of arrested growth for the plants are just as strong and as tall as others when these are about to flower; but it is due to the fact that after they have reached this stage they continue to grow vegetatively for some weeks to come. The first flower-bearing node is therefore considerably higher in *leptocarpa* than in other forms and the spike of flowers standing well above those of the other plants on the bed enables us to detect the species immediately. The stem is, moreover, rather flaccid so that the flowering spike hangs over to one side. The flowers and buds do not differ in any essential feature from those of *O. Lamarckiana*; the buds are, just before they open, a slightly brighter green with less yellow in them. The fruits and bracts on the other hand are quite different. The bracts are broader at their base, more triangular and more flattened, whilst those of *O. Lamarckiana* are often more or less bent and wavy along the midrib. They are pressed much more closely against the stem which they almost completely enclose in a mantle, as it were: instead of hanging down they stand up fairly straight. Finally

they are covered with numerous small pits which tend to alter the color of the leaf.

The fruits are long and thin, and therefore quite different from those of *O. rubrinervis.* They seldom ripen because the plant flowers so late. In November 1896 I measured the length and breadth of the first five ripe, or at any rate full grown, fruits on a number of plants of *O. leptocarpa* which occupied two beds. I divided the breadth by the length and employed the quotient as a measure of the thickness. The values which I got were quite definite; the mean thickness lay between 15 and 17 whereas that of *Lamarckiana* ranges between 22 and 24. Thus we see that the carpels of *O. leptocarpa* are about ⅔ as thick as those of the parent species.

The following are the values which I obtained:

BREADTH / LENGTH	1896 NUMBER OF INDIVIDUALS *A*	*B*
12	0	1
13	1	3
14	5	3
15	6	8
16	11	2
17	15	3
18	13	5
19	3	1
20	5	1
21	2	0
22	2	1
23	1	0
24	0	0
Totals	64	28
mean	17	15

The culture A was from the seeds of the two *leptocarpa* mentioned on p. 262; B from an artificially self-

pollinated individual in a parallel culture in the same year.

It only remains to be stated that in these two cultures the *O. leptocarpa* came true to seed. In fact this can be clearly seen from the above two columns of figures; the individuals measured obviously form a definite group, although their curve of individual variability naturally overlaps that of *O. Lamarckiana* whose mode is at 22-24. The curves are transgressive, as is so often the case in closely allied species.[1] The thickest fruits of *O. leptocarpa* are thicker than the thinnest of *O. Lamarckiana,* so that if we only had this character to go by we should sometimes be unable to distinguish the two species.

Culture A consisted of 300 and B of 150 plants and all of them, even those which did not ripen their fruits exhibited the characters peculiar to *O. leptocarpa* with the single exception of two *O. nanella.* Some of the plants were perfectly pure *leptocarpa* whilst others approached the characters of the parent species to a certain degree. For, all the characters of the species exhibit individual variability just as we have seen the thickness of the fruits to do.

In spite of this transgressive variability the constancy of the new species was proved by the cultures. There was no real reversion.

§ 17. OENOTHERA SEMILATA.

This species has only appeared thrice in my cultures; and every time from *O. lata.* One appeared in 1894, the other two in two independent cultures in 1895. They looked very much like *O. lata* except that the characters

[1] On this point see § 25 of this Part.

of that species were only slightly developed. Hence the name *semilata.* The 1894 plant was broken in a storm. One of the 1895 ones flowered well but at first set no fruit. It was not until November when it had attained a height of 2 meters that some good fruits were developed, but the oncoming winter prevented the ripening of the seed.

I was more fortunate with the third plant. It had arisen in 1895 from the first *lata-family*; and had therefore *O. lata* as mother and grandmother, and *O. Lamarckiana* as father and grandfather. See the pedigree on p. 285. At first they only differed but little from the real *lata* of the same culture, the buds were however slightly thicker, the inflorescence looser and longer, the leaves narrower and slightly more rounded at the tip. But when the flowers opened it was found that the anthers produced apparently good pollen although not so much as is produced by *O. Lamarckiana.* I then enclosed the plant in a parchment cover and selfed the flowers. I also pollinated two pure *latas* with the pollen of this plant. The pollen proved to be quite good, for in both cases the plants yielded a good harvest of seed.

I sowed the self-fertilized seeds of the *semilata* plant in 1897. The resulting culture consisted of 276 plants which flowered and 82 which did not. There occurred amongst them three dwarfs (*O. nanella*), three *lata* plants which flowered, and a rosette which evidently belonged to the same species. The *nanella* were obviously mutants, the *lata* either this or perhaps reversions. The remaining plants clearly exhibited the characters of *semilata* and justify the establishment of this form as a constant species. But I did not consider the experiment important enough to continue.

The above mentioned cross *O. lata* × *O. semilata* did not give any particularly remarkable result; amongst 105 seedlings there were 39 *lata, 2 nanella, 2 oblonga,* and 1 *albida,* whilst all the rest were *O. Lamarckiana.* These forms and the proportions in which they occur are the same as those which *O. lata* produces when crossed with other species. These figures give little support to the supposition, which is improbable on other grounds, that *O. semilata* is a hybrid or perhaps an intermediate form between *O. lata* and *O. Lamarckiana.*

§ 18. OENOTHERA NANELLA. (OENOTHERA LAMARCKIANA NANELLA.)

In view of the great importance which attaches to a satisfactory distinction between species and varieties it seems worth while to go a little closely into the difference between *Oenothera nanella*[1] and the other new species.[2]

The new species, other than *nanella,* which have arisen in my experimental garden find no analogues either in other species of the same genus or anywhere else in the vegetable kingdom. Each constitutes a new and distinct type and is, without question, to be regarded as an elementary species.

Varieties are distinguished from these in popular

[1] *Oenothera nanella,* or the Dwarf Evening Primrose, often called the dwarf for short, is a constant form. The term dwarf is often used to signify the smallest individuals, presented by fluctuating variability, which are of course of an entirely different nature. For information on such dwarfs see P. Gauchéry, *Recherches sur le nanisme végétal,* Ann. sci. nat. bot., 8 Serie, T. IX, 1899, pp. 61-156; and also D. Clos, *Du nanisme dans le règne végétal,* Acad. Sciences Toulouse, T. XI, 1889.

[2] For further details see the second volume of this work.

estimation first as being derived forms and secondly by the supposed fact that they do not come true to seed but from time to time revert to the type of the species. This latter view has long been shown to be baseless; for many varieties are just as constant as the best species. Varieties are really distinguished by the fact that the same variation recurs in a great number of species and genera. The type is not new but appears under a variety of forms.

Fig. 77. *Oenothera nanella.* Entire plants with flowers and almost fully grown fruits. 1/3 nat. size.

Let us apply this to our dwarf *Oenothera.* Dwarf varieties are as numerous as, for example, glabrous ones. The following are some well-known examples, *Tagetes patula nana, Tagetes signata nana, Scabiosa atropurpurea nana, Papaver somniferum nanum, Dianthus caryophyllus nanus, Dianthus barbatus nanus, Cheiranthus cheiri nanus, Matthiola incana nana, Calliopsis bicolor nana, Cuphea purpurea nana, Impatiens Balsamina nana* and many others.[1] Most of them are very popular garden-flowers.

[1] See List in Carrière, *Production et Fixation des Variétés,* p. 10.

From the systematic point of view therefore our dwarf should be called *Oenothera Lamarckiana nana* or as it is particularly small, *O. Lam. nanella.* But from the experimental point of view it behaves just like the other elementary species; for it is, as already stated in § 3, absolutely true to seed. And as the name *O. nanella* cannot refer to anything else I shall usually employ it.[1]

If we look a little more closely into it we shall find other grounds for regarding our dwarf as an elementary species. In the first place it is by no means a miniature edition, as it were, of *O. Lamarckiana.*

Fig. 78. *Oenothera nanella.* *A*, a seedling with two leaves; *c*, the cotyledons. *B*, an older seedling showing the long-stalked leaves or flag-leaves, of the atavistic period, which appear next after the first leaves.

On the contrary it is, like the other new species, different from it in almost all its characters. It cannot be mistaken for a weak plant of the parent species at any time. Or to express it more emphatically, if we reduce pictures of *Lamarckiana* and dwarfs to exactly the same size we find that we can distinguish them by perfectly definite characters.

[1] I recall in this connection DARWIN's aphorism: *Varieties are only small species.*

The dwarfs can be recognized not only as early as the rosette stage but even when the first leaf is developed (Fig. 78 *A*). This first leaf is broader and has a broader base and a much shorter petiole than that of *O. Lamarckiana.* The same is true of the second leaf. The result of this is a compact appearance in the young plant which makes it possible to record them in the seed pans, if the seeds have been sown so far apart that the seedlings only just touch one another. Of course there are often one or two doubtful individuals left over, as for example when the seedlings are crowded together in groups; but the doubt can always be removed by growing the plants in question a few stages further.

The stage we have just described is followed by an atavistic period. The dwarf characters disappear and it looks as if the little plants aspired to become tall *Lamarckianas.* There appear two, three, or four narrow leaves set on long petioles (Fig. 78 *B,* v. v. v.); they conceal the two first leaves which are much smaller, and so determine the general appearance of the plant for a short time. But this stage is soon shown to be a transitory one by the appearance, in the center of these leaves, of the compact rosette of the regular dwarf type. (Fig. 78 *B,* and Fig. 79 *A*).

This so-called atavistic period is very common in seedlings.[1] We are all acquainted with the fact that seedlings of species of *Acacia* with phyllodes have pinnate and doubly pinnate leaves; a fact which enables us to derive the species in question from doubly-pinnate ancestors. The seedlings of *Ulex, Sarothamnus* and those Papilionaceae which lack, or have rudimentary, fo-

[1] See the excellent summary of these phenomena in Goebel's *Organographie,* I, 1898, pp. 121-151.

liage behave in the same way.[1] Another striking example is afforded by the decussate arrangement of the leaves of young trees of *Eucalyptus Globulus,* a species which in adult life has long-stalked leaves arranged on a different plan.[2] *Sium latifolium* and *Berula angustifolia* have in adult life simply pinnate leaves but in youth the broad compound leaves which are characteristic of other Umbelliferae, and therefore evidently are like those of their ancestors. There are numerous other examples[3] of species which exhibit the characters of the systematic group to which they belong as special characters of their early stages. These are the truest cases of atavism.

The dwarf-*Oenothera* is another example of a species which behaves in this way. With this difference, that in this case the ancestry is known by direct observation whilst in the other cases it has only been deduced from a comparative study. But the important point is that in this respect *O. nanella* behaves as an ordinary species, or rather, what is much more important, that the best systematic species behave in the same way in respect of this form of atavism, as elementary forms which have just arisen from the parent type.

It is usually during this "atavistic" stage that the fate of the plant—whether annual or biennial—is decided. If the former, the stem begins to be formed almost immediately; the elongate leaves are a kind of preparation for this, for the leaves which clothe the lower part of the stem are of this form as is shown in the left

[1] J. Reinke, *Untersuchungen über die Assimilationsorgane der Leguminosen,* Jahrb. für wissensch. Botanik. Bd XXX, Heft I und 4, 1896-1897.

[2] F. Delpino, *Teoria generale della fillotassi,* Genova, 1883, p. 242.

[3] For the Conifers see L. Beissner, *Handbuch der Nadelholzkunde,* 1891.

figure in Fig. 45 on page 236. If the rosette is to become biennial and if the conditions of growth are favorable which practically means, if the rosette has plenty of room to grow in, it begins to develop broader and shorter stalked leaves and is recognizable at once, and from any distance, as a dwarf rosette. The leaves are often not much longer than 7-8 cm. at this age whereas the radical leaves of *Lamarckiana* often attain a length of 30 cm. or more.

This atavistic stage is, however, more often succeeded by a rosette stage which lasts well on into June but, if the plant is going to be an annual, comes to an end then. During this period the leaves are again very broad and attached to the short stem of the plant by a broad base. Their form is often triangular, the leaves being almost as broad as they are long. If the plants have plenty of room, the outer leaves are pressed close against the ground. The outer leaves at this stage have quite short stalks (Fig. 79 *A*), the inner ones however are almost sessile, almost ensheathing the others with their broad bases. A full-grown leaf of a rosette of this age, with its petiole is shown in Fig. 52 on page 293 at *n*.

But if the plants are growing so thickly that they are cramped for room, their whole appearance becomes quite different but none the less recognizable (Fig. 79 *B*). The leaves which make their appearance after the "atavistic" stage (v. v.) stand more or less erect, are somewhat narrower and have longer petioles but are still set on the stem by a broad base. The result is that the stalks seem to be twisted in a curious way which is not brought out clearly in the figure, but which is so characteristic a feature of the young plant that it is by this character that the young dwarfs are usually first identified; and they differ from

individuals of *O. Lamarckiana* of the same age in other respects as well. (See Fig. 64 on page 325.)

I have recorded the young plants in any one of the four stages (Figs. 78 and 79) according to circumstances. The further apart the seeds are sown the sooner can the recording be done. But even when they are sown thin a few seeds occasionally fall close together; so that we find groups of seedlings which cannot be identified until long after the others have been recorded and removed. It is often from 4 to 6 weeks before the last individuals have fully developed their characteristics.

Fig. 79. *Oenothera nanella.* Young rosettes in May and June. *A*, from seeds sown thin; *B*, from seeds sown thick; v. v. the long-stalked leaves of the atavistic period.

Indeed I have often had to transplant the seedlings before I could be certain about them: when I did this I gave them ample room and grew them for about a month more in the boxes. If I recognized a plant as a dwarf-mutant in a culture of another species I kept it until it had attained the stage shown in Fig. 79 *A*; and usually transplanted it to watch its further development. If on the other hand it was merely a question of finding out whether any *Lamarckianas* occurred in sowings of *O. nanella* (as they often did after fertilization in the open)

the recording was usually done at an earlier age. For it is obvious that the earlier this can be done the greater is the number of individuals that can be dealt with.

When the seeds are sown in beds and not in boxes, as they usually were at first, we must of course await either the full development of the rosette or if they become annuals, the production of a stem.

The characters described have enabled me to obtain the figures already given, as to the repeated appearance of *O. nanella* from *O. Lamarckiana* and from other new species. I propose to give these figures again together with results obtained in certain other cultures in order to convey some idea of the frequency of *nanella*-mutations.

The fact that they appear every year, and in numbers which become greater in proportion as the sowings are more extensive is proved by the tables given in §§ 2-7; so that I shall have no occasion to refer to it again.

INDIVIDUALS OF O. NANELLA WHICH HAVE ARISEN BY MUTATION.

I. FROM OENOTHERA LAMARCKIANA.

THE ORIGIN OF THE LAMARCKIANAS:	YEAR	TOTAL OF SEEDLINGS	NANELLA	NAN. %
Lamarckiana-family	1889-1899	50,000	158	0.3
A branch of the same	1895	10,000	111	1.1
Laevifolia-family	1889	400	12	3.0
Various crosses (p. 300)	1898	4,599	26	0.6
O. scintillans	1897-1898	1,654	15	0.9
A biennial culture	1897	1,529	9	0.6
Culture of plants with variegated leaves	1899	1,972	9	0.5
	Totals	70,154	340	0.5

The proportion of dwarfs produced by *Lamarckiana* is—if we neglect the *laevifolia*-family where it is possible that other factors may have come into play—a fairly

constant one; moreover it seems to make no difference whether the *Lamarckianas* are of pure strain or the offspring of crosses.

This conclusion is supported by the proportions in which *O. nanella* occurs in crops raised directly from crosses, that is, in the first generation after the cross. The foregoing table referred to the second generation from artificial crosses, or from free crossing as in the case of *O. laevifolia.*

INDIVIDUALS OF O. NANELLA WHICH HAVE ARISEN BY MUTATION.

II. FROM CROSSES.

CROSS	YEAR	TOTAL OF SEEDLINGS	NANELLA	NANELLA %
O. Lam. × *O. biennis*	1900	80	1	1.0
O. lata × *O. biennis*	1899	299	2	0.7
O. Lam. × *O. brevistylis*	1898	293	5	1.7
O. Lam. × *O. gigas*	1899	100	2	2.0
O. Lam. × *O. scintillans*	1899	112	1	1.0
O. lata × *O. Lam.*	1900	2000	3	0.2
O. lata × *O. Lam.*	1895–1900	2387	26	1.1
O. lata × *O. brevistylis*	1896–1899	425	6	1.4
	Totals	5696	46	0.8

If we compare these figures with those already given for other species we find a striking agreement between them and those for *O. oblonga* (about 1 %) and we may therefore regard *O. nanella* as one of the commoner forms. It may also be regarded as parallel in this respect with *O. lata* which will be described afterward (§ 22) and possibly with *O. albida* which however appears in varying proportions. *O. rubrinervis, O. gigas,* and *O. scintillans* on the other hand form a quite distinct group of rarer mutations, whilst *O. semilata* and the other less important types form a third group of still rarer deviations.

O. nanella has arisen from other new species in about the same proportions; from *leptocarpa* in 1896 in a proportion of 0.4 %, from *O. scintillans* in various experiments from 1896-1899 also in a proportion of 0.4 % (There were 29 *nanellas* amongst 7872 seedlings).

The progeny of *nanella* mutants come true to seed. I have observed over 400 examples of this species which have arisen directly from other forms. Together they obviously constitute a species which can at once be recognized by many characters, although every one of them was different from its parents and ancestors.

I have already in § 3, p. 238, given the most important facts relating to the constancy of this form. It only remains to amplify the brief account of the experiments given above.

I have made four series of experiments on the constancy of *O. nanella.* I began the first of them in 1889 with the twelve mutants from the *laevifolia*-family mentioned above (273). As I was not familiar with parchment bags at that time I was not able to guard my plants against the visits of insects although I always grew them on a bed which was isolated as much as possible. But even so, the dwarf type proved heritable in a very high degree. I harvested the first seeds in 1890 as the plants did not flower till the second year. I raised 20 plants, of which 18 were dwarfs; they flowered the same summer and set plenty of seed. This seed (about 6 ccm.) I sowed on a bed of about 4 square meters. The culture consisted almost entirely of dwarfs. After this the plants flowered regularly in the first summer so that I obtained the fourth generation in 1893 and the fifth in 1894. The third consisted of 400 plants which were practically all dwarfs; I fertilized some of these with their own pollen

by enclosing them in bags. As a result of this, absolute purity of the cultures was attained in 1894. A culture of 440 which flowered during August and September consisted entirely of dwarfs.

I have not continued this experiment further because it seemed to me more important to work with the mutants themselves and to test the constancy of the first generation.

In 1895 I used for this purpose some *nanellas* which had just arisen from the *Lamarckiana*-family, and from a branch of it. I fertilized 12 of the former and 8 of the latter with their own pollen excluding the visits of insects from them. I collected the seeds of each plant separately, sowed them in the following spring, and, after a month, transplanted all the seedlings without exception, into wooden boxes, in manured soil, where they would have plenty of room to develop into rosettes like that shown in Fig. 79 *A* (p. 366). Some of them which were too close together grew like the type shown in Fig. 79 *B*; I removed the plants which surrounded these in order that they might have room to expand their leaves in. The recording, as a result of this, took place at different times but all during the month of June.

The twenty seed parents of 1895 were raised from the seeds of nine separate plants of *Lamarckiana* of which five belonged to the third (p. 224) and four to the second generation (p. 262). The twenty mutants themselves therefore belonged to the fourth and third generations. In the following tables I denote the grandparent by *Lam.*, the parent or mutant by *Nan.*, and the seedlings raised from the seeds of these latter by S. The letters A-E refer to the five *Lamarckiana*-plants of the third generation, L-O to those of the second generation; their

children are the *nanella* mutants (*nan.*) whose seeds I sowed. The number of offspring from each separate parent are recorded in the tables.

OENOTHERA NANELLA.

OFFSPRING OF MUTANTS FROM THE LAMARCKIANA-GENERATION

THIRD			THIRD			SECOND		
LAM.	NAN.	S.	LAM.	NAN.	S.	LAM.	NAN.	S.
A	No. 1	277	C	No. 1	30	L	No. 1	55
A	" 2	124	"	" 2	21	"	" 2	99
B	" 1	89	D	" 1	80	"	" 3	302
"	" 2	66	E	" 1	38	"	" 4	22
"	" 3	292	"	" 2	71	M	" 1	30
"	" 4	68				N	" 1	339
"	" 5	34				O	" 1	105
						"	" 2	321
	Total	950		Total	240		Total	1273

Altogether there were 2463 seedlings which were all without exception *O. nanella.*

These results seem to me to justify the belief that the remaining *nanella*-mutants of 1895 would also, if I had collected their seed and sown it, have proved constant.

One thing which I learnt from these extensive sowings was that the dwarfs were recognizable, and could therefore be recorded, at a much earlier stage than I had imagined before—viz., in the pans, before the first transplanting. Now, it is just the transplanting in such experiments which is the greatest labor and it is impossible to hand it over to an assistant on account of the danger of possible mistakes, so that this discovery opened up the possibility of testing the constancy on a much larger scale.

I used for this purpose the *nanellas,* referred to on page 262, which came up in 1896 from seeds which had

remained a year in the soil. Such plants also occurred in the main culture referred to on page 224, although they are not referred to there. I selfed 38 plants, in bags, with their own pollen. They were all mutants from *Lamarckiana,* some with three, some with two generations of tall ancestors. I saved and sowed their seed separately; and recorded the seedlings at the stage shown at Fig. 78 *B*. Doubtful ones were allowed to grow a little further. The average number of seedlings from each of the 20 seed-parents was 500, the maximum was 860, and only in three cases was it less than 100.

The total number of seedlings was 18649; they were without exception dwarfs. Three of them were also *oblonga* and one also *elliptica.*

Thus the seed-parents of the second experiment proved themselves to be, like the 20 of the first, perfectly constant.

It seemed to me important to test the constancy of *nanellas* from other sources. I chose for this purpose two plants from a *scintillans*-family. This family arose from the lateral branch of the *Lamarckiana* group (p. 262) and indeed from the only individual referred to there. This was biennial and flowered in 1896. I sowed some of the self-fertilized seed of this in 1898 and selfed the *scintillans* plants again with their own pollen. From the seed thus produced I obtained nine examples of *nanella,* which I transplanted and selfed. Only two of them however set seed. They had two generations of *scintillans* behind them, and behind these two generations of *Lamarckiana.*

The plants had become very weak; and the harvest was a meagre one. Only 64 seeds germinated; but they were all *nanella.* This shows that the dwarfs even when

they arise from another new species, exhibit in the first generation not only the same characters but are as true to seed, as those which arise directly from *Lamarckiana*.

For testing the constancy of this form under self-fertilization in subsequent generations I used the second of the above mentioned experiments as a starting-point (p. 371). Some of the 2463 plants mentioned there were chosen as seed parents and self-fertilized. The seeds gathered from 4 of them were sown in 1897; they gave respectively 94, 135, 154 and 164 seedlings—547 in all—which proved without exception to be dwarfs when they were recorded as large rosettes in July. I allowed about 100 of these to flower and fertilized some of them with their own pollen. In 1898 I raised from the seed thus produced the fourth *nanella* generation which again was perfectly constant, and allowed about 100 specimens to flower. The fifth and sixth generations (1899 and 1900) also came perfectly true to seed. Of the total number of seedlings—about 400 in 1900—I allowed about 70 to flower and used about 30 of these as seed parents.

Thus from the third generation to the sixth, embracing in all over a thousand plants, there occurred no single instance of atavism. The new species must therefore be regarded as perfectly constant.

The constancy of *nanella* is however incomplete in the sense that it has inherited the capacity of mutating, from the parent species. For it gives rise to individuals which though obviously *nanellas* also betray the characters of some of the other new species.

And, conversely, it occasionally happens that dwarfs arise from other new species and then bear the characters of both types together. In this way we get species of the second order, which correspond to the cultivated varie-

ties of the second and third order as described above.[1]

Combinations of this kind occur both in pure cultures and in the offspring of crosses. The following are the cases which I have observed so far.

Commonest of all were dwarfs which also bore the characters of *lata*, developed to their full extent. I noticed the first in 1892 amongst my *nanellas*, which were at that time, as I have already stated, constant in every other respect. There were three plants which, like the rest, were annual. They flowered amongst the others and were fertilized with their pollen. They produced fruits which however contained little seed. They attained a height of 25 cm. and could be recognized even before they flowered as *nanella-lata*. Their broad rounded leaves, the compact inflorescence with broad bracts, their thick swollen buds and the crumpled petals of their flowers exactly resembled those of true *lata*. But their seeds, resulting from fertilization by *nanella*, gave rise to ordinary *nanella* only

In the summer of 1896 I had another example of *nanella-lata* from seeds of self-fertilized *nanella*. It agreed exactly with those observed in 1892.

In 1898 and 1899 the same combination appeared amongst the offspring of two crosses (I) *O. Lamarckiana* $\times$ *O. nanella*, (II) *O. lata* $\times$ *O. nanella*. In the first of these (1898) there were two examples amongst about 100 dwarfs, in the other (1899) only one amongst 133 *nanellas* and 79 *latas*. The second culture was undertaken solely with the object of bringing about the combination of the two forms by crossing. This object was attained, the characteristic features of the two pa-

[1] Compare for example *Scabiosa atropurpurea nana purpurea* and other cases on p. 197.

rents being fully developed; but only in a single individual.

Beside *nanella-lata* I have observed the following combinations:

COMPOUND TYPES OF OENOTHERA NANELLA.

FROM SEEDS OF	COMBINATION	
O. Lamarckiana × *O. nanella*	*O. nanella-oblonga*	1898
O. lata × *O. nanella*	*O. nanella-albida*	1899
" " " "	*O. nanella-elliptica*	1899
" " " "	*O. nanella-scintillans*	1899
O. nanella	*O. nanella-oblonga*	1897
O. scintillans	*O. scintillans-nanella*	1899
O. gigas	*O. gigas-nanella*	1897
O. Lamarckiana	*O. nanella-elliptica*	1889

This list is sufficient to show that the dwarf-character can be associated with the characters of the various other new species. The characters of these others may also be associated with one another although this is very rarely the case. This difference between *O. nanella* and other species is doubtless intimately connected with the varietal, as opposed to specific, character of *O. nanella* which marks it off from all the other new species.

If we regard *nanella* as a variety we should expect it to arise from any of the new species just as much as from *O. Lamarckiana* itself. And it should be noted in this connection that, of the 6 combinations mentioned, only one arose from the seeds of *nanella*.

I shall now give a description of the flowers of the dwarf (Fig. 77, p. 361).

These are remarkably large compared with the size of the plants, especially in the case of vigorous biennial individuals. On the latter they attained to very nearly the size of the flowers of *O. Lamarckiana*. On plants which flower in the first year they are usually much

smaller in correspondence with the greater weakness of the whole plant. The petals commonly measure only 2½ × 4 cm., as opposed to the 3 × 5 cm. of *Lamarckiana*.

On annual plants some of the flowers are often incompletely developed. As a rule only one or two flowers on a plant are affected in this way. Sometimes there is very little pollen, sometimes none at all; very often it happens that the stigmas cannot separate, and remain close together. This stigmatic group is often quite small and sometimes blackens and shrivels up before pollination. Or again, the style may be so short that it does not protrude from the corolla.[1]

Fig. 80. *Oenothera nanella*. Buds at the top of the stem. At the side are shown the commonest malformations of such buds.

A striking abnormality is an oblique position of the buds on the calyx tube (Fig. 80). The calyx is bent sideways in such a manner that the bud is at right angles to the calyx tube. The opening of the calyx is interfered with by this and indeed often takes place abnormally or incompletely. The petals do not unfold properly and the sexual organs are more or less sterile.

These abnormalities are usually to be found on the lower flowers when the plant has not attained a height

[1] These and other malformations of the dwarfs are often due to a disease, and as such, to a large degree dependent on outer circumstances. (Note of 1908.)

of more than 10-15 centimeters. But even the common *Lamarckiana* often produces some abnormal flowers amongst the lower ones. If the *nanella* survives this period and if it becomes markedly stronger it forms, first, a shorter or longer intermediate piece and then a fine head of large flowers. This is borne by the barren looking, bracteated, flowerless part of the stem, well above the lower half of the inflorescence. But it is by no means all plants that are strong enough to reach this state.

The best way of raising fine plants of *nanella* is to make them biennial by sowing the seed late.

C. THE INCONSTANT SPECIES.

§ 19. OENOTHERA SCINTILLANS.

(Plate V.)

As far as we know, species in nature are constant. This is true also of elementary species, and of most so-called varieties. It is true that the older systematists, such as KOCH, SPACH and many others, believed to be able to distinguish varieties from species by their inconstancy. But they seldom took the trouble to exclude the visits of insects in the numerous experiments they made. If we take this precaution many varieties prove to be as constant as species.

The universal belief in the constancy of species has led us to regard this quality as one of the attributes of a species. From this standpoint, it would seem a contradiction in terms to speak of an inconstant species.

But such a contradiction need only trouble adherents of the current theory of selection. The mutation theory can remove even this difficulty. Lack of constancy is

obviously one of the most unfavorable characters that a species can possess; and the theory of selection which can only explain the origin of favorable characters cannot account for the existence of unfavorable ones.

According to the mutation theory a species, even if it is so weak that it can hardly maintain itself, and can only just reproduce itself, is capable of existing, for a time, alongside the parent species. *Oenothera brevistylis,* which hardly sets any seed and yet has maintained itself amongst the *Lamarckianas* at Hilversum since 1887, proves the correctness of this view. At some future date no doubt, if the struggle for existence becomes keener, it will give way to *Lamarckiana* or be vanquished in the struggle with other plants whilst *Lamarckiana* may survive. But if the conditions of life remain as they have been up to now, there is at least the possibility that *O. brevistylis* may continue to exist alongside *Lamarckiana.*[1]

This difficulty can be avoided by confining the term species to those forms which have emerged victorious from the struggle for existence. But such a limitation of the meaning of the term would of course be perfectly arbitrary and only serve to further confuse a problem already sufficiently difficult.

The doctrine of mutation on the other hand makes it easy to see how species may arise and yet be disqualified for survival for any length of time. Mutability produces deviations in all directions (I, § 26, p. 198); it is absolutely uninfluenced by the greater or lesser utility of the changes it produces. It simply produces variations, leaving it to the struggle for existence to decide whether they are in the right direction or not. But the

[1] It still occurred in that locality in 1907. (Note of 1908.)

event is dependent not only on the quality of the variation but also on the environment in which it is placed. The variations which pass through the sieve of the struggle for existence are not different from, but merely part of, those which are put into it.

The mutation theory admits of the production of such forms as will sooner or later for some reason or other, perish without having contributed materially to the flora or fauna of a district. The causes of such disappearance are mainly three: (1) sterility, or at any rate insufficient fertility; (2) constitutional delicacy; (3) inability to breed true.

Nor is there any *a priori* ground for supposing that more "fit" species arise than "unfit."

There have arisen in my cultures besides robust forms like *O. gigas* and *O. rubrinervis,* and weak ones like *O. oblonga* and *O. albida,* a series of forms which were either sterile, or were fertile but did not come true to seed. I should have called them transitory species, were it not that all species are transitory. I now refer to the former group as infertile and to the latter as inconstant species.

Neither of these types can last long in nature. They must obviously be excluded from amongst the species with which the ordinary investigation of nature familiarizes us. It is only when one can witness a period of mutation that there is any chance of seeing such forms.

I propose to deal now with some types of inconstant species and shall begin with the one I have investigated most thoroughly.

This is *Oenothera scintillans* which is figured on Plate V and in Fig. 47 on page 244. I have already stated, in § 3 of this section, that the seeds of this species pro-

duce three different forms, *O. scintillans, O. oblonga,* and *O. Lamarckiana* even after it has been carefully fertilized with its own pollen and the visits of insects have been effectually excluded. The proportion in which *O. scintillans* is reproduced is in some cases about 35-40 % and in others about 70 %.

Before we can estimate the effects of this inconstancy we must know what happens in subsequent generations. I shall afterwards give the details of some experiments which show that the *O. oblonga* and *O. Lamarckiana* thus produced are as constant as those given off directly from the main stem of the *Lamarckiana*-family. The *scintillans* on the other hand behave like their parent, their offspring segregating in the same way.

What will be the composition of the successive generations? We will suppose that the plants are self-fertilized, that no selection takes place and we will put the proportion of *scintillans* in each generation at about one-third. And we will limit the extent of the generations to a thousand plants each. The contents of successive generations will, then, obviously be:[1]

	SCINTILLANS	LAMARCKIANA + OBLONGA
1st Generation	333	667
2nd "	111	222 + 667 = 889
3rd "	37	74 + 889 = 963
4th "	12	25 + 963 = 988
5th "	4	8 + 988 = 996
6th "	1	3 + 996 = 999
7th "	0	1000

Therefore in a batch of about 1000 plants all the scintillans would have died out after seven generations without the operation of any selective process. In the case before us however the process would be hastened

[1] The xth generation will contain $(1/3)^x$ *scintillans.*

by a very definite selection resulting from the fact that *scintillans* is much more delicate than *Lamarckiana.*

It is now sufficiently clear that a species which produces besides offspring like itself other constant types must inevitably disappear sooner or later.

If the constant types appear in a smaller proportion than we have considered so far, in each generation, as in the case of *O. scintillans* producing 70 % of its kind (p. 246) it will take longer for the form to disappear; but disappear it must.[1] It is only by excelling its constant offspring in individual strength that it can ever stand a chance of surviving altogether. If it did this it would be in the position in which *O. Lamarckiana* finds itself now with regard to the new species arising from it.

These facts give a simple explanation of the absence (or perhaps rather the great rarity?) of inconstant species in nature. For it is not necessary to assume that such do not arise or even that they do not arise often. The proof that they cannot maintain themselves is sufficient. Left to themselves they will be reduced in a very few years to a hundredth or even thousandth part of the total of their offspring, and they will very soon be lost altogether. They can only continue to exist by being produced continuously or, at least, frequently by the parent species.

The mutation theory renders the origin and disappearance of unfit types intelligible; moreover the actual origin of such has been observed. These cases constitute an insuperable obstacle in the way of the theory of selection.

[1] The 12th generation will bring the form down to about 1 %; and generally speaking the xth to $(^{7}/_{10})^{x}$.

From these general considerations I pass on to the special treatment of our first example *O. scintillans.* Fig. 47 and Plate V show the flowering spike of annual examples of the species; the long, tapering budbearing internodes above the open flowers cannot fail to attract attention. This feature stamps the habit of the plant from July to late in the autumn: in most of the other species the buds do not rise much above the crown of flowers. Moreover the bracts in this region are pretty

Fig. 81. *Oenothera scintillans. A,* young plant with 6 leaves above the cotyledon. *B,* young rosette at the age of two months.

large so that the youngest part of the stem is fairly thickly clothed with leaves.

The flowers are considerably smaller than in *O. Lamarckiana,* a circumstance almost certainly due to the general delicacy of the species. Otherwise, the structure of the flowers resembles that of the parent species; for example the stigmas extend well beyond the anthers so that the flowers are generally cross-fertilized.

The development of the anthers and the pollen is to a high degree dependent on external conditions. The pollen is sometimes plentiful, sometimes scanty, and at other times entirely absent. These variations occur on one and the same plant and seem to depend chiefly on the temperature, inasmuch as the anthers degenerate under the influence of hot weather. It is in consequence of this circumstance that I have lost many fruits by enclosing flowers in parchment bags (to insure pure self-fertilization) in the full sunlight.

Fig. 82. *Oenothera scintillans.* A rosette of radical leaves, at the end of June.

The annual plants are only very slightly branched, and begin to flower when they are only ½ meter high. The lateral branches spring from just underneath the flowering zone, and on them isolated flowers appear towards the end of September or even later. Biennial plants are usually more branched, and if the heart of the rosette happens to have frozen in the winter a circlet of

secondary stems is formed. Biennial plants are in every respect stronger and bear larger fruits with better seeds.

But the most characteristic feature of this species is its smooth shining dark-green narrow leaves.

The young rosettes are recognizable by this character (Figs. 81 and 82), and can easily be distinguished by means of it from the species by which they happen to be surrounded (Fig. 52, p. 293).

The leaves are not very narrow at first; in fact they do not become so until the rosettes are 2 or 3 months old. This feature gradually becomes more pronounced during the summer whether the plant remains in the rosette stage or develops a stem. The midrib of the leaf is broad and like the leaf stalk is of so pale a green that it might almost be called white, and has not a trace of red color in it. The leaves of the full grown rosette have long petioles and are about four times as long as they are broad or even narrower. There are no unevennesses on the blade nor is there that pale green bloom on them which is characteristic of *O. albida* and *O. rubrinervis;* they are almost absolutely smooth and very different from those of *Lamarckiana* in their dark green color. Indeed, *scintillans* bears very little resemblance to its parent species except in its flowers.

The leaves of the stem (Fig. 54, p. 295) resemble those of the rosette in all essential points and so do not require any special description.

In regard to the mode of its origin *O. scintillans* resembles *O. gigas* and *O. semilata* in being one of the rarest types. It has only arisen 14 times altogether as a mutation. Although most of these instances have already been described it is worth while summarizing them all here.

OENOTHERA SCINTILLANS.

INDIVIDUALS THAT HAVE ARISEN BY MUTATION.

SOURCE	YEAR	TOTAL OF SEEDLINGS	O. SCINTILLANS	PRODUCING RIPE FRUIT
O. lata	1888	—	1	1 (2)
The *Lamarckiana*-family	1895	14,000	1	0
	1896	8,000	6	2 (2)
	1897	1,800	1	0
Lateral branch of this family	1895	10,000	1	1 (2)
O. Lam., a subsidiary culture	1897	3,000	2	0
O. lata	1898	164	1	1 (1)
O. lata × *O. biennis* . . .	1899	300	1	0

As the last column of the table shows I only succeeded in getting ripe fruits from five of these mutants, of which four set seed in the second year (2) and only one in the first (1). The rest died as rosettes or at any rate before they fruited. The percentage composition of the cultures raised from these seeds has already been given on pp. 244-246, but will be described in greater detail now.

I shall begin with the oldest. It appeared in 1888 in the *lata*-family referred to on p. 288; it was biennial and flowered luxuriantly in July 1889 but was left to be fertilized promiscuously amongst a crowd of *Lamarckianas*. It had all the characters which were afterwards observed both in its offspring and in the other mutants. I sowed its seed partly in 1890 partly in 1894 and obtained, in both years, both annual and biennial plants. The rosettes of 1894 flowered in 1895; the plants were self-fertilized in parchment bags. There were 14 healthy plants, bearing hardly any branches: their fruits were small, and did not afford more than 1 to 3 cubic centimeters of seed per plant. The seeds were sown on sep-

arate beds and the young plants recorded at the end of June.

As the seeds were sown thin and as a great many did not come up, the seedlings stood far apart and had plenty of room in which to develop their characteristic features.

I counted:[1]

	PER SEED PARENT	TOTAL	IN %
Seedlings	16—52	399	—
O. scintillans	2— 9	62	15
O. Lamarckiana	7—36	268	68
O. oblonga	1—11	60	15
O. lata	0— 2	8	2
O nanella	0— 1	1	—

This experiment showed that each of the 14 seed parents gave rise to the three chief forms, when self-fertilized. They did this moreover, so far as the small numbers enable us to judge, in not very widely different proportions.

In this experiment the original mutant was fertilized by insects; but all the subsequent mutants which appeared were enclosed in parchment bags, as soon as they began to flower, and artificially self-fertilized. The first to be treated thus was the *scintillans,* mentioned on p. 262, which appeared in 1896 in a branch of the *Lamarckiana*-family. Six stems were developed from the axils of its radical leaves and a quantity of seed was set. I also succeeded in taking cuttings from the remaining branches of the rosette: they survived the winter and flowered in the following year. I sowed the 1896 seed partly in 1897 and partly in 1898, in the former year both in pans and in a bed in the garden. The three crops raised in this way were composed as follows:[2]

[1] See the table on p. 244. [2] See the second table on p. 245.

	1897 IN PANS	1897 IN THE GARDEN	1898 IN PANS
Number of seedlings	572	275	165
O. scintillans	36 %	34 %	36 %
O. Lamarckiana	52 %	52 %	60 %
O. oblonga	10 %	13 %	3 %
O lata	1 %	1 %	1 %
O. nanella	1 %	0	0

In the summer of 1897 I selfed five of the *Lamarckianas* in this culture with their own pollen. Each bore from 12-13 cm. of seed, of which some was sown next year in the garden and in pans. 117 seeds germinated in the garden and 1079 in the pans. There was not a single example of *scintillans* amongst these. The majority of them were *Lamarckianas,* with a considerable admixture of mutants. In the garden these were, 4 *O. rubrinervis,* 3 *O. lata,* 1 *O. nanella,* 1 *O. albida* and 2 *O. oblonga*; in the pans the only mutants were 7 examples of *O. nanella.*

The *Lamarckianas,* therefore which are produced by *O. scintillans,* have the same constancy as the original *Lamarckiana,* that is to say their grand-parents, but also exhibit the same degree of mutability.

The point is that a continued segregation into *Lamarckiana, scintillans* and *oblonga* is not witnessed in the seedlings from the *Lamarckianas* extracted from *scintillans* as it was in the original *scintillans.*

Of the mutants mentioned *O. rubrinervis, O. lata* and *O. nanella* flowered the same summer.

The very important question now presented itself, how the *scintillans* plants in this generation behaved on self-fertilization. To answer this question I enclosed over 50 plants of the 1898 culture in bags. harvested their seed separately and sowed it. All the seedlings

were transplanted, under glass at first, in order to give them plenty of room for the full development of the rosette. The rosettes were counted between the ages of 2 and 3 months, the process lasting from the middle of May till the middle of June (see Fig. 82). Altogether about 5850 rosettes produced by 42 plants were recorded. The crops which contained less than 50 seedlings from a given parent were recorded but not included in those from which the following percentages were counted. The average number of seedlings per parent plant in the cases dealt with is therefore about 140.

The number of *scintillans* naturally varied from crop to crop, as a result, doubtless, of the smallness of the number of seedlings counted. I have determined the percentage values for each parent, and arranged them in groups of 1-10 %, 10-20 % and so on. I found:

	NUMBER OF SEED PARENTS
7 %	1
19 %	1
21—30 %	9
31—40 %	12
41—50 %	15
51—55 %	4

This gives an average of 40 %, a figure which agrees with the coefficient for the grandmother (36 %) closely enough.

The *oblongas* in this experiment varied between 0-12 per seed parent. There were 197 of them altogether, i. e., they formed about 3 % of the population. The rest were, with the exception of about 1 % *O. lata* and *O. nanella,* all *O. Lamarckiana.* We have therefore on the average:

	SECOND GENERATION	FIRST GENERATION
O. scintillans	40 %	36 %
O. Lamarckiana	56 %	60 %
O. oblonga	3 %	3 %
O. lata and *nanella*	1 %	1 %

The agreement between the two succeeding generations is as great as can be expected in an experiment of this kind.

There were four seedparents with 52, 52, 54 and 55 % *scintillans* in, respectively 111, 61, 161 and 95 seedlings. The *scintillans*-producing capacity seems very variable, but the figures would perhaps deviate less if greater numbers had been grown. The deviation seems, however, to lie within the limits of individual variability.

In 1896 six plants of *O. scintillans* arose in the main line of the *Lamarckiana-family* (p. 224 and 385). I succeeded in bringing two of these through the winter and in getting them to flower in 1897. Their pollination was artificial and not disturbed by the agency of insects. The amount of seed set was small, varying from ½ to 2 ccm. per plant: is was sown, separately for each seed parent, in March 1898.

One seed parent gave rise to 365 seedlings which included the same types in the same proportion as in the previous experiment.[1] The other yielded a total of only about 200, which was, however, made up quite differently.[2] 69 % of the population were *scintillans,* that is to say twice as much as in the previous experiments. The relative number of *oblonga* was also doubled and amounted to 21 %. The number of *Lamarckianas* was correspondingly low, amounting to no more than 8 %,

[1] See the numbers on the lower table on p. 245.

[2] P. 246.

whilst that of the other mutants (*O. lata, O. nanella,* etc.) remained at about 2 %.

There is therefore in *O. scintillans* a highly fluctuating degree of the hereditary capacity, if by this term we may denote the different proportions in which *O. scintillans* is able to produce offspring like itself.

The hereditary capacity can either be very small, or about 35-40 %, or as much as 69 %; the latter figure being about twice as large as the former. In the case of the former this capacity was essentially the same in the second generation as it was in the first, and in the case of the latter the difference was also very little.

This is proved by the result of the continuation of the experiment we are dealing with (See p. 246). In 1898 about 30 plants were self-fertilized; they yielded a poor harvest. The crop raised from 26 of them consisted of about 2200 plants, i. e., about 90 per seed parent. The hereditary values for each of these are arranged in the following list in groups, as before.

% SCINTILLANS	NUMBER OF MOTHER PLANTS
66—69 %	2
71—74 %	2
76—80 %	5
81—85 %	6
86—90 %	9
92—93 %	2

The average is 84 % and therefore even higher than the 69 % of the previous generation.

The average composition of the whole culture from the 26 parent plants of 1898 was:

O. scintillans	84 %
O. Lamarckiana	13 %
O. oblonga	2 %
O. lata	1 %

The amount of *O. oblonga* has greatly decreased, whilst that of *Lamarckiana* has somewhat increased (see p. 246).

In the summer of 1899 I again selfed a whole series of plants in this culture. I selected these from the offspring of two plants which had produced respectively 87 % and 90 % *scintillans* and seemed, therefore most likely to breed true. I only fertilized *scintillans* plants. The yield, however, was very poor; 10 seed parents only giving more than 60 seedlings each. These could be recorded in June and showed high hereditary coefficients:

MOTHER	NUMBER OF SEEDLINGS	% SCINTILLANS
1	146	86
2	122	91
3	113	76
4	112	92
5	98	89
6	96	87
7	77	83
8	75	80
9	74	81
10	68	74

The whole crop raised from the seeds of the 29 plants gave:

	NUMBER OF SEEDLINGS	%
O. scintillans	1126	79
O. Lamarckiana	93	6
O. oblonga	209	15
Total	1428	

These figures agree almost exactly with the mean value of the culture in the previous generation in spite of the fact that I began the culture with two seed parents with exceptionally high *scintillans*-producing capacity, viz., 87 % and 90 %, and irrespective of the fact that

the proportions for the other mutants seem to have been inverted.

This result tends to prove the correctness of the conclusion, suggested above (p. 389), that the deviations from the mean hereditary coefficient are phenomena of fluctuating variability and have nothing to do with mutation.

The fifth mutant of *O. scintillans* from which I was able to get seed arose in 1898 from the *lata*-family described on page 285. There was only one plant which unlike all the previous ones developed a stem very early and flowered in the first summer. It was self-fertilized in a bag, set little seed and gave rise in 1899 to 148 identifiable plants of which 37 % were *scintillans.*[1]

This is another example of the hereditary coefficient exhibited by two of the three other mutants which were tested—a particularly interesting case because the origin of this *scintillans* was quite different from that of the others and the plant was an annual.

I shall now summarize these coefficients.

SOURCE	YEAR OF MUTATION	SCINTILLANS PLANTS		
		2nd gen.	3rd gen.	4th gen.
O. lata	1888	—	15 %	
O. lata	1898	37 %		
O. Lamarckiana	1895	34—36 %	40 %	
O. Lamarckiana	1896	39 %		
O. Lamarckiana	1896	69 %	84 %	79 %

These figures seem to be arranged in groups of 15 %, 34-40 %, and 69-84 %. It would obviously be very important to determine more of these figures in the case of a large number of *scintillans*-mutants; if this were done the groups will probably turn out to be more vari-

[1] See the first table on p. 245.

able, or even wholly illusory. Perhaps we might even get a constant race of *scintillans.*

§ 20. OENOTHERA ELLIPTICA.

Almost every year there appear amongst my plants isolated individuals with very narrow leaves. There are three types of such. First those in which the narrowness is the result of some malformation. Sometimes one half of the leaf in this case is more reduced than the other and the leaf is consequently more or less deformed. Plants of this kind sooner or later return to the normal type of *O. Lamarckiana,* and behave afterwards just like this. The narrowness is presumably in this case a pathological phenomenon; I shall not deal further with it.

The two other types are constant and maintain the character throughout life. One of the forms has long leaves which are broadest in the middle and gradually taper off to the tip and to the stalk. I call this form *O. elliptica.* The other, a much rarer form, has linear, almost grasslike, leaves and will be described in the next section under the name of *O. sublinearis.*

The seedlings of *O. elliptica* are recognizable at a very early age (Fig. 83 *B,* to be compared with Figs. 64-66, pp. 325-326). Its leaves have long petioles and are very narrow, seldom attaining a breadth of more than 0.5-0.7 cm. for a length of 8-10 centimeters. One result of this is that they assimilate much less carbonic acid than *O. Lamarckiana,* so that they are weak and very easily overgrown by their normal neighbors. But even when they are transplanted early and treated with every possible care they grow very slowly. The plant shown in Fig. 83 *B* was photographed in July.

The great majority of the new mutants of this species stayed in the rosette stage their first year; but they were so delicate that I did not succeed in wintering them.

Fig. 83. *Oenothera elliptica.* *A,* twig of an adult plant, (1895); *B,* a seedling of 1893; *C.* radical leaf of a full grown rosette.

Others developed stems but did not flower. I have only seen flowers on ten plants altogether and only obtained seed from five of these.

Even when they flowered the plants were still delicate: their leaves retained the long narrow shape (Fig. 83 *A*). The plants do not as a rule attain a great height but are profusely branched and are so unlike an *Oenothera Lamarckiana* that they do not look as if they could be any relation to it. So unlike, indeed, are they that the seedlings ran the risk of being taken for weeds and thrown away.[1]

Fig. 84. *Oenothera elliptica.* An open flower, to show the rounded tips of the petals, (1895).

But the flowers reveal its kinship with *O. Lamarckiana* at once. They are large and fine, much larger indeed for so weak a species than our experience of *O. oblonga, O. scintillans* and others would lead us to expect. They have the same structure as those of the parent species; the stigma extends well above the anthers and so cannot be fertilized without the help of insects or of the experimenter. The shape of the petals however is different, as will be made sufficiently evident by a comparison of Fig. 84 with Fig. 42 on page 218. The petals of *O. Lamarckiana* are broader than long, indented at the tip and so more or less obcordate. In the open flower their margins overlap so that a closed cup is formed. The petals of *O. elliptica* are elliptical;

[1] This circumstance considerably increases the work in my experimental garden. Weeding ought only be done by assistants who can assign individual plants to their species and can be trusted to spare unknown forms. For the rarer a mutant is the more likely is it to be taken for a weed. For this reason, I have usually done this work myself.

their greatest breadth is about their middle or slightly above this and they are rounded at the tip. They are very like the autumn flowers of *O. laevifolia.* (Fig. 59, p. 312), only that they have this shape from the beginning of the flowering period. And just as the shape of the petals in *laevifolia* in autumn may be ascribed to the diminished supply of nutriment at that time of the year, so there is very probably some causal relation between the shape of the petals and the narrowness of the leaves in *O. elliptica.*

The pollen was frequently empty, but this also happens occasionally in other species as in *O. scintillans* and even in *O. gigas.* It is quite normal for numerous species of *Oenothera* to have a large proportion of sterile pollen, as for example in *O. biennis L.* and *O. muricata L.* The fruits of *elliptica* were small, and contained little seed.

The origin of *O. elliptica* has already been noted in the pedigrees of the various families (Part II, §§1-7). Here is a summary of these cases:

FAMILY	YEAR	NUMBER OF O. ELLIPTICA
O. Lamarckiana, a branch of the main family,	1895, 1896	8
O. laevifolia	1889, 1891, 1893, 1894	7
O. lata	1900	1
O. lata	1890	2

I have not entered the occurrence of *O. elliptica* in the pedigree of the *Lamarckiana*-family (p. 224); its occurrence in the various years in which it appeared was as follows:

	YEAR	NUMBER OF O. ELLIPTICA
2nd Generation	1888	2
3rd "	1890	2
6th "	1896	7

O. elliptica occasionally appeared in other cultures. Here are some examples.

OENOTHERA ELLIPTICA.

INDIVIDUALS THAT HAVE ORIGINATED BY MUTATION.

SOURCE	YEAR	NUMBER OF SEEDLINGS TOTAL	NUMBER OF SEEDLINGS O. ELLIPTICA
O. Lamarckiana (subsidiary cultures in the *laevifolia*-family)	1889, 1891, 1893, 1894	3200	6
O. Lamarckiana (from *O. scintillans*)	1898	1080	2
O. oblonga	1896	1680	1
O. Lamarckiana × *O. nanella*	1899	3815	1
O. Lamarckiana × *O. brevistylis*	1898	290	1
O. Lamarckiana × *O. suaveolens Desf.*	1897	200	1
	Totals	10265	12

This is a proportion of about 1 in a thousand. It appeared in similar proportions in other cultures. Altogether rather more than 50 mutants have arisen.

This species flowered in 1890 (1), 1891 (1), 1895 (3), 1896 (3), 1897 (1), that is, only tentimes altogether. I obtained seeds from the three plants of 1895, and from those of 1896 and 1899; in all of which cases self-fertilization had taken place under bags.

The first plant of 1895 set seed abundantly, and gave rise to some hundreds of seedlings, which grew to fine rosettes but proved however to be ordinary *Lamarckiana.* Many of them flowered in their first summer, but others passed through the winter as rosettes.

The second mutant had about 500 offspring; one of these was an *O. elliptica* which had become a fine rosette by the middle of August but was then killed by a caterpillar in the soil. The remaining seedlings were normal *Lamarckianas.*

The third plant of 1895 set little seed and only gave rise to 27 seedlings not one of which was an *elliptica.*

The mutant of 1896 was an extraordinarily beautiful plant with narrow leaves and narrow elliptical petals, and altogether absolutely unlike an ordinary *Oenothera.* Its fruits were long and thin and contained but few fertile seeds. 32 seeds germinated; 27 of the plants they gave rise to were *O. Lamarckiana,* the remaining 5 were *O. elliptica*—that is about 15 %. These five plants developed stems, but did not flower till November: they were exactly like their parent. Their leaves did not exceed 2-3 cm. in breadth, the petals were elliptical and without the emargination at the tip. They did not set seed.

The last mutant which bore seed was a plant which arose in 1899 from seed of *O. scintillans.* It appeared in the culture of 5850 rosettes (p. 388) which gave 40 % *O. scintillans* in the third generation. This culture contained only one *O. elliptica,* which, as it was transplanted early, grew up into a plant which branched profusely and flowered freely but was of rather low growth. Its leaves were very narrow but its flowers relatively large. The breadth of the petals on this plant was highly variable. Its fruits were slender and contained but little seed. Abut 100 seeds germinated, but gave rise solely to rosettes of *O. Lamarckiana.*

To sum up: the hereditary coefficient for *O. elliptica* was 0 in three cases, 1 per 500 in one case, and about 15 % in the remaining one. The first three plants had only a few hundred offspring between them, and this fact in itself may be sufficient to account for the non-appearance of *ellipticas* amongst them. If this is really the case the last two mutants (with 0.2-15 %) may provisionally be regarded as representing the normal.

§ 21. OENOTHERA SUBLINEARIS.

This form differs from the last named chiefly by its grass-like leaves which are very narrow and of equal breadth along their whole length (Figs. 85 and 86). The foliage leaves are longer and markedly narrower; the

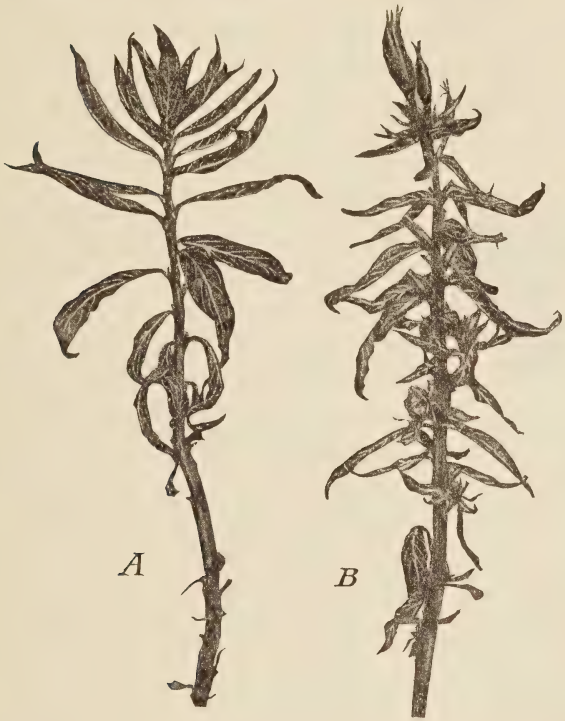


Fig. 85. *Oenothera sublinearis.* Two annual plants, at the end of August 1900. *A,* without, and *B* with flower buds.

Fig. 86. *Oenothera sublinearis* A radical leaf, 1895.

foliage on the stem is dense and not scanty; the fruits are short, and not slender as in *O. elliptica.* Although I have had very few examples of this species so far, it is evi-

dently a genuine well-characterized type; the herbarium specimens and photographs I have kept of the first that appeared agree perfectly with the mutants which have arisen since.

The flowers presented no differences from those of *O. elliptica.* They are the same size, that is, are somewhat smaller than those of *O. Lamarckiana,* but large when the weakness of the species is taken into consideration. The petals are not obcordate but narrower at the extremity, and rounded or sometimes even pointed at the tip. The stamens and stigmas resemble those of the parent species.

Fig. 87. *Oenothera sublinearis.* Petals with a stamen, July, 1896. From the same biennial plant as Fig. 86.

Examples of *O. sublinearis* appeared in my cultures from year to year, but the majority of them perished as young rosettes. Only four plants grew beyond this stage and only one of these afforded fertile seed, which when sown produced the new form in the proportion of 10 %. In this respect it falls therefore into the same category as *O. scintillans* and *O. elliptica.*

The history and fate of the four mutants which produced stems must now be briefly described. I shall begin with the single plant which set seed.

This plant arose from seed of the *Lamarckiana*-family which had been sown in 1895, but had remained in the ground for a year. It was recognized in June 1896 as a peculiar form and transplanted separately. It was biennial and flowered in 1897 on its numerous lateral branches which however bore only a few flowers each. The whole plant was short and stunted, and its

flowers were relatively large. They were self-fertilized in parchment bags. But the harvest was very scanty. Only 31 seeds germinated, and these were transplanted with the greatest care and cultivated further.

The composition of the progeny was by far the most varied that I have observed; there occurred:

19 *O. Lamarckiana*	1 *O. albida*
3 *O. sublinearis*	3 *O. subovata*
1 *O. lata*	1 *O. gigas*
1 *O. nanella*	2 *O. oblonga*

I weeded out the *Lamarckianas* as strong rosettes at the end of June, when there could no longer be any doubt as to their identity. The *O. sublinearis* and *O. subovata* remained in the rosette stage and died in the winter. All the remaining plants flowered, some in August and September, and some (*O. gigas*) in November of the same year. Their identity with plants grown from the seed of mutants of the same name was fully established especially in the case of the rarer forms *O. albida* and *O. gigas.*

This extraordinary richness in mutants is probably connected in some way with the smallness of the harvest as was believed to be the case in the experiment described on page 264. This highly important point needs further investigation.

The second plant belonged likewise to the *Lamarckiana*-family; it appeared in 1895 and flowered in 1896. One of its first year's radical leaves is shown in Fig. 86, two of the petals which it bore in 1897 are shown in Fig. 87. The plant was pale green and so weak that there seemed very little chance of its surviving the winter. But it flowered rather well: there were about a

dozen flowers on two stems which arose from the axils of its radical leaves. These attained a height of about half a meter. But in spite of all the trouble I took I got no fertile seed from it.

The third mutant arose in 1900 in the first *Lata*-family, as already recorded in the genealogical table on p. 285. It is figured in Fig. 85 *B*. It was planted out in June, grew well, but remained short and did not branch. It bore large flowers and small fruits and was cut off at the end of August to be photographed.

The fourth mutant (Fig. 85 *A*) arose from a cross between *O. rubrinervis* and *O. nanella,* which was made in 1899. It developed an unbranched stem, which attained a length of about half a meter, in its first year, but it did not flower.

D. THE STERILE SPECIES.

§ 22. OENOTHERA LATA.

One of the most difficult questions which the mutationist has to answer is that which refers to the nature of the fundamental process, involved in mutation, the visible results of which are the peculiarities and characters by means of which the new form is distinguished from the parent species. I have already laid stress on the fact, which has not escaped the notice of the best workers in this field, that elementary species are not distinguished from one another by one character only, as varieties are, but by almost all their organs and characters. This is not only true of the elementary species, in a state of nature, which have been described by JORDAN, GANDOGER, THURET, DE BARY, ROSEN and many others but also of those which have arisen in my cultures.

I hold that all the new characters of a mutant are manifestations of a single change that has taken place within it. Morphological proof of this thesis can as yet hardly be produced, but physiologically it follows of necessity, in my opinion, from the fact that these characters are always associated and, so far as our experience goes, cannot be separated.

Fig. 88. *Oenothera lata.* A lateral branch at the end of August just opening its first flower.

Oenothera lata is perhaps the most beautiful example. I have already described the characters peculiar to it in § 3 on pages 239-243 (Fig. 46), but I propose now to elaborate that description. In the first place it is one of

the commonest mutants, and at the same time one of the most easily recognizable in its early stages. It appeared 229 times in the main line of the *Lamarckiana*-family (p. 224), in the branch family 171 times, in the *laevifolia*-family 9 times and very frequently in other cultures too. I have cultivated many such mutants until they flowered and set seed; in every case they conformed exactly to a common type.

No separation of the characters of the species has been observed. *Oenothera semilata* (§ 17) which appeared at first to be an instance of this, turned out to be a distinct form.

The characters of the species can be regarded as distinct "groups," better in the case of *O. lata,* than in the case of any other species. Each "group" obviously constitutes a unit, but how the existence of the separate "groups" is brought about by the same cause is as yet unknown. Examples of these "groups" are, the form of the leaves, the thick flower-buds, the lack of pollen, the abnormal growth of the pistil, and the short fruits with relatively few seeds.

Let us look at the leaves; they are crumpled, and round at the tip; the edge is too small for the area of the leaf which is therefore much bent. The bracts are much broader at the base than they are in the parent species. The apices of the large branches and the smaller lateral branches form peculiar little rosettes. A complete description would extend over a whole page of print and need many figures. (Fig. 89.) Nevertheless it is certain that all these units are intimately bound up with each other and that they must owe their existence to the presence of a single factor.

Perhaps this factor is the abnormally luxuriant super-

ficial growth of the leaf parenchyma in proportion to that of the nerves; but perhaps we must seek deeper for it.

It is not, however, easy to see how the same cause can make the stigma abnormal, the fruits small and the pollen sterile. On the other hand if we suppose that each

Fig. 89. *Oenothera lata.* A, a radical leaf. B, the bract, from the axil of which the lowest flower arose. C, apex of a small lateral branch. A', B', C', the corresponding parts of *O. Lamarckiana* diminished the same amount.

of these characters is due to a distinct cause we have no means of accounting for the fact that they always appear together and never one at a time: for this clearly could not be due to chance.

I imagine that the cause of every such a mutation

is a single one; though its real nature is not yet apparent to us. But this much is clear, that it is not, at least as a rule, manifested as a single quality. And in this respect a mutant differs from a variety, in which single qualities like color, hairiness and so forth form the diagnostic character. In the mutant this quality can only be manifested in connection with the older characters of the plant; and the total expression of this cause must therefore depend partly on the older characters and only partly on the new factor itself.

If we look at it in this way we can easily imagine how a single internal change can bring about the abnormal development of the leaf parenchyma, of the pollen cells of the anthers, of the petals, the fruits and the stigmas, and in this way produce the broad crumpled leaves, the sterility of the pollen, the thickness of the buds and the abnormal stigmas.

This is of course only an idea. I mention it partly to simplify the problem and partly because it may indicate the lines along which the problem may be dealt with empirically. In order to make my position clearer I will now tentatively indicate the parallel which exists between this idea and certain phenomena of parasitism. It is generally admitted and, indeed, there can be little doubt that the wonderfully definite and complicated structure of the Cynipid-galls, with their nutrient tissue, their stone-cells and their spongy tannin-containing outer parenchyma[1] whose thickness is adapted to the length of the ovipositors of parasites and Inquilinae, cannot be the result of a single chemical stimulus. But it is an entirely different matter with the cases of virescence since these

[1] M. W. Beyerinck, *Beobachtungen über die ersten Entwickelungsphasen einiger Cynipiden-Gallen.* Verh. d. K. Akad. d. Wet., Amsterdam, 1882.

are evidently only useful to the parasites in quite a general way. The virescence of *Lysimachia vulgaris,* which is occasioned by a *Phytoptus,* affords perhaps the most beautiful example of a complete series of transitions from flowers to leafy branches.[1] This change is obviously the object of the stimulus given by the Acarine and it obviously does not matter whether the number of the changed petals of the corolla varies or not. Nevertheless these and other monstrosities accompanying the virescence are by no means rare.

The case of the virescence on the galls of *Aulax Hieracii,* in the flowerheads of *Hieracium vulgatum, H. umbellatum,* etc., which have been studied by Treub, is very instructive.[2] These galls are usually situated in the stems far away from the flower, but in rare cases they occur in the flowerhead itself. When this happens the flowers are affected by a whole series of the most remarkable malformations which begin by the calyx producing little green sepals. These changes are obviously of no use to the Cynipids which live inside the galls; for the *Aulax* larvae grow just as well if no inflorescences are borne on the galls.

Galls not rarely evoke monstrosities of this kind, provided of course that the potentiality for these monstrous growths already exists. I have found, for example, a stem of *Hieracium vulgatum* which was normal below the gall but, above it, was broadly fasciated. In the summer of 1887 I saw several stems of *Eupatorium cannabinum* bearing, about their middle, galls of *Pterophorus microdactylus*: below these the leaves were green

[1] A. B. Frank, *Pflanzenkrankheiten,* 1880, p. 691.

[2] M. Treub, *Notice sur l'aigrette des Composées, à propos d'une monstruosité de l'Hieracium umbellatum,* Archives Néerlandaises d. sc. phys. et nat., T. VIII, p. 1 and Plate I.

but above them they were variegated. The gall stimulus, therefore, does not exert its influence only on those qualities which are necessary for the formation of the galls, but on others as well.

The effect of a single mutation on the most diverse and important, as well as on subsidiary, qualities may be of a similar nature as that of a gall stimulus. But if it is difficult to discover the chemico-physiological nature of the gall stimulus; it is wellnigh impossible to penetrate into the mystery of the chemical nature of a primary mutation.

Let us now make a more detailed study of the characters of our *Oenothera lata* and let us begin with the stamens. The anatomical structure of these has been investigated by Prof. J. Pohl[1] (Fig. 90), partly on the plants of my first *lata*-family (p. 285) in 1894, partly on a larger culture which I raised in that year from the seeds of the second *lata*-family (seeds of 1889 and of 1890, see p. 288) and partly on isolated new mutations. The structure of the stamens was the same in all cases; and was, therefore, independent of the ancestry of the plant.

Pollen formation takes place in *Oenothera Lamarckiana* and *O. lata* in the ordinary way; the mother cells enclosed in the tapetum each divide into two daughter cells and each of these into two granddaughter cells. The loculus increases in capacity by the dissolution of the tapetum; and the further development of the pollen-grains takes place in the fluid which now surrounds them. The ripe pollen of *O. Lamarckiana* consists of two forms

[1] Julius Pohl, *Ueber Variationsweite von Oenothera Lamarckiana;* Oesterr. Botan. Zeitschr., 1895, Nos. 5 and 6, and Plate X.— See also R. R. Gates, *Pollen Development in Hybrids of Oenothera lata*; in Botanical Gazette, T. 43, p. 81. (Note of 1908.)

of grains, about 70% large normal grains,[1] the rest being small grains poor in protoplasm. The pollen of *O. lata* on the other hand consists of crumpled, distorted grains which form every conceivable transition between absolutely empty sacks and apparently normally developed grains. But the empty ones and the almost empty ones are in the majority; the apparently well developed ones occurring only sparingly amongst them. Moreover the viscin threads, which in *O. Lamarckiana* connect all the pollen-grains together so that they form a sticky mass, appear to be absent. The open anthers feel dry and if they are touched with the finger, bits of sticky masses of pollen do not adhere to it.

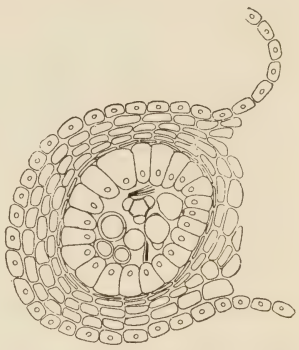


Fig. 90. *Oenothera lata.* Transverse section of an anther, showing the large cells of the tapetum. After J. Pohl, Oesterr. Bot. Zeitschrift, 1895, Plate 10, Fig. 28.

If we follow the development of the anthers in *O. lata* in a series of buds of increasing size we find that development is normal up to about the stage of tetrad-formation. Shortly after this stage dissolution of the tapetum takes place and there are found floating in the lumen, besides apparently normally developed tetrahedral pollen grains, some quite round, others invaginated on one side.

I devoted a great deal of time in 1894 to trying to fertilize *O. lata* with its own pollen, trusting that the few apparently good pollen grains which I had found would be able to effect fertilization. I plastered as much

[1] Figured by Luerssen in Pringsheim's *Jahrbüch.*, Vol. VII, pp. 35-42, and Plate IV, Figs. 1-14 (Pollen of *Oenothera biennis*).

pollen as I could on the stigmas of a few flowers; but all to no purpose. Then, as it was difficult to liberate the pollen direct from the anthers on to the stigma, I teased it out with needles on to a glass slide, collected it in a lump and transferred it direct from this to the stigma—but, again, all to no purpose.

After this I pollinated the flowers, without castrating them, with the pollen of a remotely related plant, belonging in fact to another subgenus; *O. odorata.*[1] I have obtained fertile crosses between this form and *O. Lamarckiana, O. biennis* and *O. muricata.* It ought, then, to be able to fertilize *O. lata* also; but my attempts to effect this were practically without result although I pollinated many flowers on four plants. Only a single seed germinated; and this produced a hybrid plant. This experiment also shows that self-fertilization did not occur.

Besides this I have pollinated castrated and non-castrated flowers of *O. lata* with the pollen of *O. Lamarckiana.* I have also tried the effect of putting very little *Lamarckiana*-pollen on the stigmas of uncastrated flowers in the hope that perhaps I might induce self-fertilization in that way. All these experiments gave exactly the same result; about 15-20% of the seeds gave *O. lata,* the rest *O. Lamarckiana.*

I conclude from these and from a number of other experiments that the pollen of *O. lata,* in spite of the presence of occasional apparently good grains, is nevertheless absolutely sterile. One result of the establishment of this fact is that the castration of flowers of *O. lata* in hybridization experiments becomes unnecessary.

[1] From the subgenus *Oenothera* (*Euoenothera*); whilst *O. Lamarckiana* etc. belong to the subgenus *Onagra.*

If there had been evident signs of the existence of pollen in individual flowers among the numerous mutants and their offspring which I have artificially fertilized during the course of the last six years, I must certainly have seen it. But this has never been my lot.[1]

The stigmas have also been figured and described by Pohl.[2] They differ from those of *O. Lamarckiana* by their tendency to be confluent with one another and with the style. Their number is variable, as in the parent species, where 4 is the normal; but numbers up to 8 are

Fig. 91. *Oenothera lata.* Young seedlings. A, showing the cotyledons and the two first leaves. A', natural size. B, with 7-8 leaves (⅔) two months old, seen from above. The tear in the leaf to the right was caused by trying to bend the leaf flat.

not rare. As result of the concrescence just mentioned, there arise in *O. lata* curious hand-shaped deformities. The individual fingers of these hands are sometimes free but sometimes fused to their tips. This deformity goes hand in hand with a shortening and thickening and also with a crumpling of the individual stigmata. The capacity for taking pollen and for permitting the normal development of the pollen tube, does not, however, seem to have been impaired by these malformations.

[1] As already stated, I have lately raised a hybrid of *O. lata* which produces some fertile pollen, which I have now in cultivation. See Section I, § 3. (Note of 1908.)

[2] Julius Pohl, *l. c.* p. 8 and Fig. 27.

The fruits are short and thick and contain little seed. They attain scarcely half the length of those of *O. Lamarckiana* but are almost as stout as these.

I first observed the above mentioned deviations from the type of *O. Lamarckiana* in 1887 on the very first mutants, as far as they could be discovered without mi-

Fig. 92. *Oenothera lata.* Rosette with radical leaves. Aged about 3 months.

croscopical investigation; and since then I have observed them every year not only in the new mutants but also in their progeny.

Like *O. Lamarckiana, O. lata* is both annual and biennial. But I grow it as an annual by preference. The first two leaves which appear after the cotyledons plainly

reveal the identity of the species (Fig. 91 A). The tips of the leaves are rounded and not pointed, which makes them shorter. About a month after germination this character is so clearly expressed that I choose this stage for sorting out the *Lamarckianas* from the *latas* in the results of crosses. This form of the leaf is maintained through the whole life of the rosette (Fig. 92) and on the lower part of the stem.

The wrinkling and distortion which so detract from the beauty of the leaves in *O Lamarckiana* are much more pronounced in *O. lata*; and are very rarely absent (Figs. 57 and 58, pp. 310 and 311). This feature may be brought about by the relatively small margin of the leaf.

On the whole, the abnormal breadth of the leaves is maintained up the stem even to the tops of the inflorescences and branches (Fig. 89). But, as in the case of *Lamarckiana* itself, the leaves become gradually more pointed and narrower the further up they are. Our figure (Fig. 89 A, A′) brings this out very clearly; a fine point is seen on the otherwise rounded tip of the leaf. If we look at the lowest leaf which bears a flower in its axil or an immature fruit and compare it with a corresponding leaf on a *Lamarckiana* plant (Fig. 89 B, B′), we shall find that the relative breadths are as 4 to 3. Higher up in the inflorescence this difference increases; the leaves, from whose axils the flowers which open in August arise, are about twice as broad as the corresponding ones in the parent species. And if we look at a small branch from above it looks like a thick rosette of broad leaves (Fig. 89 C) whereas in such a view of *Lamarckiana* the leaves are reduced to small and narrow bracts forming a kind of rosette of pointed leaves.

The tops of the flowering branches are also densely clothed with leaves (Fig. 88).

The remarkable thickness of the buds is clearly brought out in our figures (Fig. 46 on p. 241). The petals have not sufficient room for development in the thick but short bud: they acquire in this way folds and wrinkles which, even when the flower is fully open, are never completely lost. As a result of this the flowers are always rather unattractive, and not nearly so large and bright and widely opened as in the parent species.

The stem and branches in *O. lata* are weak, often bent downwards with the tops heavily laden and usually needing a stake to prevent their falling over. The lateral branches flowering in September are frequently seen to hang downwards; thereby heightening the characteristic appearance of the species. The plants do not as a rule attain a great height; seldom more than half that of *O. Lamarckiana.*

With all these peculiarities *O. lata* is perhaps that one of the new species which differs most widely from the parent form. Moreover it can be recognized in its earliest youth no less certainly than easily (Plate IV and Fig. 48 on p. 280). Doubtless as a result of these circumstances it was the first mutant which I noticed, and the only one which I found in my first crop of 1887. Since that date it has appeared every year as a mutation. And as it can be seen so early in each crop and as, therefore, it is not likely that it will be overlooked to any large extent, the proportions in which it appears may be regarded as established on a sufficiently firm basis to admit of a comparison between the small differences in its "mutation coefficients" (See p. 338). I found that these numbers vary considerably, often sink-

ing to 0.01% or less, or mounting to 2% or more. External conditions therefore probably affect the proportion in which *O. lata* arises from *O. Lamarckiana.* What these conditions are is a subject for future enquiry. Perhaps they exert their influence only during the ripening of the seed or during germination (See p. 263) but probably they come into play at or before fertilization.

In order to give some idea of the range of variations of these "mutation coefficients" I give a list containing the figures which have already been given (§§ 2-7) together with some new observations.

INDIVIDUALS OF OENOTHERA LATA WHICH HAVE ARISEN BY MUTATION.

LAMARCKIANA FROM:	DATE	TOTAL	SEEDLINGS O. LATA	% LATA
I. FROM O. LAMARCKIANA.				
Main line of descent, p. 224	1888–1890	25,000	8	0.03
" " " " "	1895	14,000	73	0.5
" " " " "	1896	8,000	142	1.8
" " " " "	1897–1899	3,500	6	0.2
Lateral branch, p. 262	1895	10,000	168	1.7
An annual culture	1897	4,132	11	0.3
A biennial culture	1897	164	8	5.0
II. FROM CROSSES.				
O. Lam. × *O. nanella*	1897–1899	8,283	22	0.3
O. Lam. × *O. gigas*	1899	100	2	2.0
O. Lam. × *O. biennis*	1900	80	1	1.0
O. Lam. (from crosses; p. 300)	1896	4,600	7	0.2
III. FROM OTHER FAMILIES.				
O. Lam. from *O. laevifolia*	1889	400	3	0.8
O. laevifolia	1894	1,500	2	0.1
O. rubrinervis	1894	96	2	2.0
O. scintillans	1896–1899	7,872	38	0.5

If we examine these figures closely we make rather an interesting discovery. A high figure (5%) is only

given by a culture of strong biennial plants, carried out with the utmost care (1897). Three of the figures, viz., 1, 2, 2% are afforded by too small crops to be of any significance. On the other hand the cultures of 1895 and 1896 which involved 8000, 10,000 and 14,000 plants respectively, and may therefore be relied on, gave 0.5, 1.7 and 1.8% apiece. These, then, are the most reliable figures with which the rest, with the exception of the first named (5%) agree very well. The remaining figures, which are 0.3—1—2—2—3—3—5—8 per 1000, were either obtained in earlier years or in special cultures.

In the whole table there are 493 *lata*-mutants amongst about 130,000 seedlings, or about 0.4%.

§ 23. INCIPIENT SPECIES.

According to the mutation theory, natural selection chooses between species; some are eliminated by it, others permitted to increase and multiply. The new forms arising from a single parent species by mutation may be very numerous; they are often equally well equipped for the struggle for existence being distinguished from one another by characters which are unimportant in this respect, as in the familiar case of *Draba verna.*

But should there have arisen from *Draba verna,* besides the elementary species now existing, others less fitted for the struggle for existence, they would most certainly have been eliminated sooner or later. And there is no reason for supposing that elementary species different from those now existing have not been produced.

I have seen almost every year in my cultures of

Oenothera unfit mutations of this kind, and very often in considerable numbers. For the sake of completeness I shall describe some of them here. They are not distinguished from the "fit" new species by any sharp line of demarcation, and perhaps there exist amongst them some forms from which, by the help of better methods, it may some day become possible to obtain constant types.

They are the beginnings of new species from which, for one reason or another, I have not succeeded in obtaining the species themselves. For example it was only after a series of the most laborious experiments which extended over about 6 years that I was able to get *O. albida* to flower and set seed (§ 15, p. 349). I shall therefore refer to these forms as "incipient species."[1]

My incipient species were more or less aberrant types and exhibited few points of resemblance with the new species hitherto described. Of late years I have devoted much energy to their cultivation, but with varying results.

Many of them died as young rosettes; others formed fine thick clusters of root-leaves, but developed no stem. Some I was able to bring through the winter, others perished in their first year. Many of them flowered, in some cases as early as August, in others not till autumn. If the latter happens there is no prospect in our climate of ripening seed; when the former was the case I always enclosed the flowers in parchment bags in order to insure self-fertilization. But as the pollen was usually sterile the operation was commonly fruitless. I then tried using the pollen of *O. Lamarckiana* or that of some other new species but with no better success; the ovaries seemed incapable of being fertilized.

Sterility is well known to be a highly variable char-

[1] *Ebauches d'espèces,* of some French authors.

acter. It certainly is in the *Oenotheras.* The older species *O. biennis, O. muricata* and *O. Lamarckiana* always produce, so far as we know, a pollen of which some part, often as much as one-third, consists of sterile grains. It would be very useful if some one would determine the degree of this fertility; it would without doubt follow QUETELET'S law of fluctuating variability and would probably exhibit also partial variability in a high degree—since the percentage of sterile grains would be likely to be high on weak lateral branches.[1] Sterile or almost sterile individuals may therefore appear from time to time. For example I once found a plant of *Oenothera gigas,* which, in spite of repeated attempts to fertilize it with its own pollen, set no seed. And *Oenothera brevistylis* is much more often than not absolutely sterile, in spite of the full development of its pollen; and this sterility is closely correlated with the individual variability in the size of the fruits.

It may happen that a new species absolutely lacks pollen, as we have seen to be the case with *O. lata.* But it does not follow from that, that every new form that arises, if we find it first as a sterile plant, must, when it arises once more, be sterile again.

The incipient species in my cultures were as a rule represented by solitary individuals. In rarer cases the new form was represented in the same crop by two or three seedlings; or was repeated in succeeding years. If nothing more than rosettes of radical leaves were produced, absolute certainty as to the identity of the type was of course out of the question; but it is always better in cases like these to unite those which apparently belong

[1] See amongst others A. JENCIC, *Untersuchungen über den Pollen hybrider Pflanzen,* Oesterr. Bot. Zeitschr., T. 50, 1900.

together than to multiply new types indefinitely. For these unsuccessful incipient species have hardly any further signification than that of supporting the thesis of indiscriminate mutability.

This is my chief reason for describing here in some detail a few such incipient species. For this purpose I select three of those which I have noticed, and shall call them for the sake of convenience by ordinary specific names. They are *O. spathulata,* of which I obtained only rosettes of radical leaves, *O. subovata* which flowered several times, but was always sterile, and *O. fatua* which though it branched freely has produced practically no flowers so far.

Fig. 93. *Oenothera spathulata.* A radical leaf, $^2/_3$ natural size.

Besides these three types there was a whole series of other forms which do not seem to me to be worth either naming or describing.[1]

Of *O. spathulata* I obtained two rosettes of root-leaves in the *laevifolia*-family in 1889, (p. 273); seven rosettes in 1890 in the main pedigree of the *Lamarckiana*-family; and one in a lateral branch of this family in 1895 (p. 262).

Repeated appearance in different and mutually independent families is thus established in the case of this rare new species. The plants of 1890 were fine strong rosettes about the end of June; they grew healthily through the whole summer but died in the winter without having developed a stem. I have kept some of their leaves and photographed them (Fig.

[1] Some of my new species have not arisen from the pure stock of *O. Lamarckiana* but have arisen from crossed seeds of various ancestries. Both sterile and fertile forms have arisen in this way.

93). The petiole was very long, gradually merging into the blade of the leaf; the latter attaining its greatest breadth near its rounded apex.

Fig. 94. *Oenothera fatua.* A branch in autumn with numerous flowerless bracts.

Another mutant with similar leaves flowered in the same summer; it had little flowers and empty anthers; but I was not sure whether it belonged to the same type.

I gave the name *O. fatua* to a plant which arose in 1896 from the *Lamarckiana*-family: it proved a biennial and branched profusely in 1897. It bore numerous inflorescences with green bracts, but no flowers (Fig. 94).

In the summer of 1896 I had isolated the rosette as a new form; the leaves were oval and obviously different from those of *O. Lamarckiana.* It grew vigorously in the second year, attained a height of about a meter, produced more branches than any other form I have seen and developed the most extraordinary profusion of inflorescences. It was not until late in the autumn that it began to develop normal flowerbuds, too late for them to open.

I have observed isolated examples of similar plants on other rare occasions.

My last example is *Oenothera subovata* which first appeared in 1889; and, afterwards, as isolated examples in various cultures, from time to time. Four of these mutants have flowered; the rest died in the rosette stage.

Fig. 95 is a photograph, taken in the same way as those already given for other mutations, of a group of young plants which were raised from the seeds of *Oenothera lata* fertilized by *O. Lamarckiana,* and were planted out in early spring, in rows, in boxes containing good

Fig. 95. A mutation in the *lata*-family. From a photograph taken on the 25th of May 1900. In the right column there can be seen at the top *O. albida,* in the middle *O. lata,* and at the bottom *O. albida* again. In the second column *O. Lamarckiana, O. oblonga* (in the middle) and *O. Lamarckiana.* In the third row *O. lata* (below), *O. oblonga,* and *O. subovata* (at the top, very small). In the left row three *O. lata,* and in the middle, the largest rosette, *O. Lamarckiana.* The *O. lata* and *O. Lamarckiana* are like the two parents, the rest have all arisen as mutations.

soil. It shows some of the mutations which arose from the main stem of the *lata*-family (as given in detail on page 285), and happens to be a group in which many new forms are growing close together. The figure shows

besides *O. lata* and *O. Lamarckiana* two examples of *O. albida,* (to the right), recognizable by their small narrow leaves, and two of *O. oblonga* (in the middle) which can hardly be distinguished from the surrounding examples of the parent species in the picture. The majority of the *lata*-plants photographed flowered afterwards. The *albidas* and *oblongas* grew as far as the rosette stage, but died in the course of the summer. The *Lamarckianas* were not planted out.

The *O. subovata* (the second from the left in the top row) was noticeable very soon after transplanting by the fact that it remained very small whilst the other plants grew vigorously. Its leaves were almost orbicular and were shortly petiolate. It was planted out at the end of April in a separate bed with the other mutants, and grew up to a strong full rosette with numerous ovate leaves with long petioles which distinguished it at once from all the other plants in the same bed. It died in the autumn.

The two other examples of *O. subovata* (mentioned on page 285) died in the latter part of the summer after they had formed thick rosettes similar to those already described (see also Fig. 48 on page 280).

I had, before this, observed one or two instances of rosettes with the same form of leaf and of the same general appearance. For example in 1895 I observed seven of them amongst 14,000 seedlings of the main trunk of the *Lamarckiana*-family, that is to say 1 per 2000 (p. 224). They survived the autumn, but not the winter. Then there were the three mutants (mentioned on page 401) which arose in 1898, from the seeds of *O. sublinearis* and two others which arose from *O. scintil-*

lans. And last of all, two rosettes from seeds of *Oenothera lata* fertilized by *O. biennis.*

I obtained altogether four flowering plants of *O. subovata,* one in 1889 and 1895, and two in 1899. The former arose from *Lamarckiana*-seeds, was annual, freely branched but dwarfed. It developed not only a main stem, but lateral ones from the axils of its radical leaves. Only a single one of these latter bore normal flowers like the parent species. The other lateral branches and the main stem however were quite sterile. Instead of flowers in the axils of the leaves there were little green leafy shoots (Fig. 96) which gave the plants a most singular appearance.[1]

Fig. 96. *Oenothera subovata.* A barren stem, 1889.

The mutant of 1895 arose from the *Lamarckiana*-family and flowered in August of its first year. The flowers were of the same form as those of the parent species; but, in correspondence with the greater delicacy of the plant, smaller. Later on, however, it became stronger and the flowers which were borne on its lateral branches at the end of September were quite as large as those of *Lamarckiana.*

[1] This foliation was due to internal causes and not a pathological virescence like that which may be brought about by parasites (*Phytoptus,* plant-lice, etc.). I have occasionally seen examples of this

The two *subovata*-plants of 1899 belonged to the *lata*-family. One arose from *lata* crossed by *O. nanella,* the other from *lata* crossed by *O. Lamarckiana.* Both were recognized while young plants; they developed stems and flowered freely. The first was weak and had relatively small flowers; the second was strong and bore flowers as fine as those of *O. Lamarckiana.* Both were absolutely sterile, at first I fertilized them with their own pollen and later with foreign pollen, but in both cases without result.

But I regard it as extremely probable that I shall some day succeed in getting a *subovata* that will bear seed. And if *subovata*; why not other forms which have not been detected, or even have not yet arisen in my cultures?

latter in my *Oenothera*-plants (*Botan. Jaarboek*; Gent, 1896, p. 88). But the effects of it, especially the actual virescence of the flowers themselves bore no resemblance to the peculiarities of the plants described above.

III. THE SYSTEMATIC VALUE OF THE NEW SPECIES.

§ 24. THE NATURE OF THE BOUNDARIES BETWEEN RELATED SPECIES.

It follows directly from the doctrine of mutation that the species which arise by mutation are as sharply distinguished from one another as are neighboring species of recognized systematic value.

The previous chapter has shown us that new species are, as a rule, from the very beginning as constant as other species. This constancy is manifested in two ways. In the first place the various individuals of the new species are absolutely alike in all their essential features: and this is true not only of the offspring of new mutations and of others which arise from the same parents, but also of the hosts of mutations which have arisen from widely separated and independent families of the same parent species. In the second place they come true to seed, they do not revert to the parent form. If the latter character is absent as in the case of *Oenothera scintillans* the new form cannot be capable of existence in nature and therefore cannot be compared with true wild species.

The object of the present chapter is to show that the characters of the new species which have arisen in the

genus *Oenothera* possess the same systematic value as those which distinguish the species of LINNAEUS and later systematists. I shall confine myself to the nearest relatives of *O. Lamarckiana,* that is to say, to the subgenus *Onagra.* In this way I shall have the advantage of dealing with very well known forms (*O. biennis L., O. muricata L., O. suaveolens Desf.,* etc.) and of using them as subjects of comparison. The new species differ in some respects as much, in others more, in yet others less from one another and from the parent species than these recognized forms do amongst themselves.

And first I must emphasize two things which make the treatment of this subject a difficult matter. I mean, our present wholly insufficient knowledge of the units of which the characters of organisms are built up, and secondly the phenomenon of transgressive variability.[1]

I believe that each new mutation is brought about by a single new quality (see page 403). This inner or primary quality then comes in contact with the qualities which are already present in the various organs and it is this interaction to which its particular external manifestation is due. The nature of the outward and visible form therefore depends only partly on the mutation but partly also on the characters already existing in the organism. Or, in other words, the new species is marked not as a rule by a single new peculiarity but by the transformation of many or all of its organs, more or less.

So long as we do not know the single causes in question we must compare these visible transformations in new mutations with the visible differences between old established species.

Transgressive variability is one of the main supports

[1] See page 56, and the following section.

of the current theory of selection. It makes it possible to pick out series of individuals which belong to related but different species and (being careful to choose suitable characters) to arrange them in such a way that they form a perfectly continuous series from one end to the other. If no gaps have been left in such groups by the death of species or if there are sufficient species left, perfectly continuous series of this kind can be arranged of almost any desired length.

But, as a rule, this can only be done by dealing with single characters and by not being particular about the number of individuals which go to form the successive steps in the series.

An example will make my meaning clear. *Oenothera Lamarckiana* differs from *O. biennis* by the beauty and size of its flowers. The two species can be distinguished at a great distance. The petals of the former are twice as long as those of the latter. But in both species the length is variable and follows QUETELET's law of individual variability, being in a high degree dependent on nutrition. Petal-length also exhibits partial variability and is especially low at the end of the flowering period when the plant is exhausted by bearing seed. The smallest flowers are found on the main stems of plants which are nearly over, on small lateral branches or on individually weak plants: the largest on well nourished plants just beginning to flower, or on vigorous lateral branches of large plants which through some accident or other have lost their main stem. This is true both of plants in the field and of those in the garden.

If now we choose the largest flowers of *O. biennis* and the smallest of *O. Lamarckiana,* we shall find that

this character of petal length overlaps in the two cases.[1] For in these extreme cases the flowers of *biennis* are actually larger than those of *Lamarckiana*.[2]

If we have collected a number of flowers including such extremes, it is obviously an easy matter to arrange an unbroken series with the smallest of *biennis* at one end and the largest of *Lamarckiana* at the other. The limits between the two species cannot be detected in such series even by the practised eye. And yet *O. biennis* and *O. Lamarckiana* never merge into one another.

If we wish to extend the series we can do so by adding the small-flowered *O. muricata* to it in exactly the same way.[3] And, if we leave relationship out of account, we could extend continuously down to *Oenothera minutiflora* with its flower no longer than a millimeter. Such series can be arranged for almost any character in the vegetable kingdom and in infinite variety.[4] They confuse the limits drawn between related species as far as the several characters are concerned.

If, in the classification of animals and plants, we fix our attention on a single character we shall always encounter long unbroken series of this kind. The shells of snails and the wings of butterflies are examples. It

[1] That this must generally be the case may be derived from the law of variability. Imagine two curves of variation drawn on the same abscissa. The greater the number of individuals included the further will the limits of the curves extend until they, first, touch and ultimately overlap. It is further obvious that the likelihood of this happening, even with a small number of individuals depends directly on the closeness of the tops of the curves (the mean values of the characters) and on the amplitude of the curve, or the degree of variability (Q).

[2] Examples in the following section.

[3] See the following section.

[4] For example the narrowest leaves of *Typha latifolia* are narrower than the broadest leaves of *T. angustifolia*.

is only when we compare other characters as well that we can distinguish the individual species.

The object of exact inquiry should be first to collect as many of these continuous series as possible; but second to analyze them into their component units.

This analysis can be effected both by the statistical and by the experimental method. Let us examine the former first.

A transgression of the limits is only exhibited by isolated and relatively few individuals; the vast majority belong to the mean type of the species. Therefore if we take care not to be too much on the lookout for transitional forms, or even, if we try to make our measurements as numerous as possible, the separate curves will become discernible. The result will be exactly that which we got from an investigation of the *Oenothera* flowers, namely curves with numerous apices, such as those with which the work of Bateson, Ludwig and others has made us familiar. Each apex indicates a group of individuals which belong together, to a type, or even to an elementary species.

Transitional forms can then be recognized immediately by their rarity. It becomes obvious that the transitions are only apparent and that no real continuity between the different centers of variation exists. These curves show no more than that the edges of neighboring curves on the same abscissa may overlap.

The simplest way of making the experimental method clear is to take the case of the *Oenothera* flowers again. We collect the seeds from the fruits of two flowers of equal size of which one is one of the largest flowers of *Oen. biennis,* the other one of the smallest of *Oen. Lamarckiana.* There can be no doubt what the plants raised

from these seeds will be like. The result can indeed be predicted pretty accurately by means of the law of regression (see pp. 73, 120 et seq.). The seeds of the *biennis*-flower will give plants whose flowers revert to the mean of the type of *biennis*; the seedlings of the *Lamarckiana*-flower will revert to the normal of that species.

In other words: if we are in doubt as to the nature of individuals which stand at the boundary between related species, the offspring produced after the self-fertilization of the individuals in question will settle the difficulty. Two plants which are absolutely identical in respect of any particular character may be proved by their progeny to be fundamentally different. And if, as often happens, two related groups only differ in a single character their extreme variants may be indistinguishable. Yet their seed will prove them to be intrinsically different.

The study of the limits of species is by no means solely a descriptive one. Classifications based on no more than an examination of a series of forms have no more than a transitory value.[1] Statistical methods[2] will reveal where the boundaries are: experimental methods must be called in to decide in individual cases.

§ 25. TRANSGRESSIVE VARIABILITY.

The general conclusions arrived at in the foregoing section may now be illustrated by numerical data. The determination of the nature of the limits between related species is one of the most difficult parts of the task of the

[1] De Candolle, *La Phytographie*, p. 80

[2] C. B. Davenport, *Statistical Methods with Special Reference to Biological Variation.*

systematist. The vast majority of systematic species are made and described on a few specimens; and where large numbers of individuals have been available the investigator has contented himself with the general impression they produce on him. The result of this is that we have a knowledge of the typical forms of species but no exact idea of their limits.

Statistical investigation, as we have already said, is necessary to determine what these limits are.[1] Such investigation teaches us not only what the mean of a character is, but also the range of its variation. In the foregoing section we have seen that the deviations are often so large that neighboring curves sometimes overlap. This is the phenomenon which I call *transgressive variability*.

Let us choose a particular example to make this phenomenon clear.

We will select the common species *O. biennis L.* and *O. muricata L.* which, as every one knows, can be easily distinguished by the size of their flowers. In the former species they are large and project horizontally from the stem; in the latter small and erect.

But let us subject this familiar and obvious and convenient distinction between two species made by LINNAEUS himself[2] to statistical analysis.[3] We measure the

[1] Beautiful examples of transgressive curves are given in a zoological article of P. P. C. HOEK, *Neuere Lachs- und Maifischstudien* in Tydschrift d. Nederl. Dierk. Vereeniging. (2) VI, 3, S. 231-235. See further G. DUNCKER, *On Variation in the Rostrum in Palaemonetes vulgaris.* Americ. Naturalist, Vol. 34, No. 404, 1900 and of the same author: *Variation und Asymmetrie bei Pleuronectus flesus L.,* Wiss. Meeresunters. Helgoland, Bd. III, Heft 2, 1900.

[2] SPACH in his monograph of this genus also separates these two forms as species (*O. vulgaris, Spach.* = *O. biennis L.* : *O. chrysantha Spach.* = *O. muricata L.*).

[3] The types indicated in this book by the names *O. biennis* and *O. muricata* are those found all over Europe, which are probably the prototypes on which LINNAEUS based his descriptions. In Amer-

sepals, the corolla, and the calyx-tube for a certain number of flowers; a very great number is not necessary. We plot the measurements as in the table on page 433, writing opposite each length the number of flowers which possess it. In the case of *O. biennis* I measured one flower per plant; in *O. muricata* I did the same (I) but in the case of a few plants several per plant (II). All the examples of both species come from the same wild locality, a sandy spot near Zandvoort (Sept. 1894). See table p. 433.

The measurements[1] show in the first place that the mean length of calyx and corolla for *O. muricata* at that locality is about 14-15 mm. and for *O. biennis* about 19-20 mm. They confirm the alleged difference between the two species. But they show, further, that this difference is by no means such that all of the flowers of *O. biennis* must necessarily be larger than those of *O. muricata* or that in any given case mere size would settle the question of their specific identity. On the contrary the largest flowers of *O. muricata* are larger than the smallest flowers of *O. biennis*.

The mean differences are fixed and typical. But the extreme variants overlap—the variability is transgressive.

But must we conclude from this that there is no boundary between the two species, that they merge into one another? Not at all. For the flowers were picked on undoubted *muricata*- and *biennis*-plants.

Or we may express the case thus: the limits of the

ica numerous other elementary species of both groups are found, but they have not yet been described or named. (Note of 1908.)

[1] I have given above similar data for the fruits of *Oenothera leptocarpa* (See page 357).

LENGTH OF CALYX.

Millimeters	*Muricata* I	*Muricata* II	*Biennis*
8	0	1	—
10	2	1	—
11	1	3	—
12	2	6	—
13	6	13	—
14	13	24	2
15	**20**	**35**	7
16	6	11	3
17	3	7	9
18	4	0	8
19	—	—	**9**
20	—	—	8
21	—	—	4
22	—	—	6
23	—	—	1
24	—	—	1
25	—	—	1
26	—	—	3
27	—	—	1
28	—	—	1
33	—	—	1
Flowers,	57	101	65

LENGTH OF COROLLA.

Millimeters	*Muricata* I	*Muricata* II	*Biennis*
8	0	1	—
10	1	0	—
11	3	6	—
12	8	4	—
13	12	21	—
14	14	**34**	1
15	**16**	29	4
16	3	5	6
17	—	1	6
18	—	—	9
19	—	—	9
20	—	—	**12**
21	—	—	5
22	—	—	3
23	—	—	1
24	—	—	6
25	—	—	1
Numb. of flowers	57	101	63

species overlap but they will not disappear. And, conversely, the homogeneity of an unbroken series of forms cannot be taken as established until it can be shown that the forms are grouped round a single center. The existence of two such centers may point to the existence of two distinct types, even though they seem to merge into one another.

A comparison of the length of the calyx tube in the two forms leads to the same conclusion. The plants all come from the same locality, and the flowers were all plucked from the main stems.

LENGTH OF THE CALYX-TUBE.

Millimeters	*O. muricata*		*O. biennis*
	I	II	
21	0	1	—
22	1	0	—
23	0	0	—
24	1	2	—
25	3	6	—
26	6	8	—
27	8	11	—
28	8	15	—
29	12	15	—
30	10	17	—
31	4	15	1
32	3	7	2
33	1	1	2
34	0	1	2
35	1	1	0
36	0	1	1
37	—	—	0
38	—	—	3
39	—	—	3
40	—	—	4
41	—	—	3
42	—	—	3
43	—	—	1
Number of flowers	58	101	25

Large numbers of such tables could be made; and the result would be well worth the labor if they demonstrated, as they most certainly would, that the universality of the law of transgressive variability is no argument against the independence and immutability of species.

Let us now examine a second group of characters, namely those which do not separate related species or at any rate only to a very slight extent. In this case the mean values will either coincide or show slight differences caused by external conditions. For example I found

the seeds of *O. biennis* and *O. muricata* almost exactly alike as to shape and size in spite of the considerable difference between the seeds of a single fruit. The same is true of another well-known character, the relation between the length of the corolla and that of the filaments. I measured this in ten flowers of *O. muricata* and in twenty of *O. biennis* and found the mean for the former species to be 14.6 and 8.3; for the other 10.0 and 5.5 mm., in both therefore a proportion of 100 : 55. In *O. Lamarckiana* however this proportion was 100 : 44.

The length of the fruits is dependent to a large extent on the conditions of life. If we examine plants which have been grown under diverse conditions, we find differences in the lengths of the fruits and we get series of figures which bear a superficial resemblance to the foregoing ones but are due to different causes. See the table which follows. I measured the fruits in the ripe, practically dry condition, using in each plant the lowest capsule on the main stem; the plants were collected in wild localities, but in various places. The differences have no specific value and are manifestly due to conditions of nutrition. An opposite result might have been obtained under reversed conditions.

Space does not permit me to deal in the same way with the variability of the new species which have arisen from *Lamarckiana*. The great majority of the characters are without doubt transgressively variable; unbroken series could be easily made with the leaves of *O. sublinearis* at the one end and those of *O. lata* at the other; or with the fruits of *O. oblonga* at the one end and those of *O. rubrinervis* at the other. But whenever a sufficient number of individuals are dealt with, curves derived from this material are found not to be monocentric but

LENGTHS OF THE FRUITS OF THREE SPECIES OF OENOTHERA IN MILLIMETERS.

(*O. muricata* 1894, the rest in 1893.)

Millimeters	*Lamarckiana*	*Biennis*	*Muricata*
15	1	—	—
16	1	—	—
17	5	—	—
18	11	1	—
19	17	4	—
20	27	9	—
21	37	13	—
22	62	10	—
23	74	23	2
24	**83**	24	1
25	79	28	3
26	51	30	6
27	43	**36**	12
28	32	32	18
29	18	27	34
30	13	21	**36**
31	5	22	34
32	5	26	32
33	3	28	24
34	1	7	14
35	—	5	5
36	—	6	2
37	—	3	2
38	—	1	2
40	—	0	1
Number	568	356	228

polycentric, each individual species forming a perfectly definite group. The character of each group is given by the center of greatest frequency, independently of the apparent absence of definite limits.

§ 26. OENOTHERA LAMARCKIANA SERINGE.

Oenothera Lamarckiana belongs to the subgenus *Onagra* which some authors separate into a distinct genus.[1]

Its most important distinguishing characters lie in the seeds which are irregularly angular with ridges along the angles and relatively smooth spaces in between (Figs. 97 and 98). These characters make it possible to distinguish them easily from the seeds of all other subdivisions of the genus *Oenothera*,[2] which are either smooth except for small indentations, or with a sort of crown at the upper end. The epidermis of the seed of *Ona-*

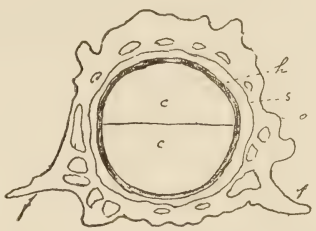


Fig. 97. Transverse section through the seed of *Oenothera Lamarckiana*; *c c*, the cotyledons (there is no endosperm); *o*, epidermis; *s*, areolar tissue with cavities; *h*, hard layer; *f f*, wings of the seed.

[1] The most important special literature on this group is the following:

E. Spach, *Monographia Onagrearum*, Nouv. Ann. Mus., IV, 3, 1835.

S. Watson, *Revision of the Extra-tropical North American Species of Oenothera.* Proceed, Am. Acad. of Arts and Sci., Vol. VIII, 1868-1873.

Engler und Prantl, *Die natürl. Pflanzenfam.*, III, 7, p. 199, where references to general literature will be found.

The following works must also be mentioned:

J. Torrey and Asa Gray, *Flora of North America*, Vol. I, 1838-1840, p. 492.

A. S. Hitchcock, *Les Oenothéracées du Kansas*, 1898.

H. Léveillé, *Monographie du genre Oenothera* (as yet only partly published).

Onagra is given as a subgenus in Endlicher, *Genera Plantarum*, p. 1190 sub No. 6115; as a genus in the *Natürliche Pflanzenfamilien* of Engler und Prantl, *l. c.*, p. 214; and also in Britton and Brown, *An Illustrated Flora of the Northern United States, Canada and the British Possessions*, Vol. II, 1897, p. 475.

[2] The various subgenera of *Oenothera* are often accidentally mixed up in botanical gardens but the above mentioned characters of the seeds usually make it possible to sort them out again before sowing.

gra which is smooth at first, grows much faster than the parts inside so that it acquires wrinkles and folds by the pressure of the surrounding seeds (Fig. 98). As a result of this there is great diversity in the form of the seeds of the same loculus. In this respect the seeds of the various species of *Onagra* are practically all alike.

The fruit is an erect capsule which splits longitudinally and contains many seeds. The flowers have a long calyx-tube, are tetramerous and apparently regular but exhibit as a matter of fact, a slight degree of zygomorphy which is most pronounced in the filaments. Prophylls are absent.

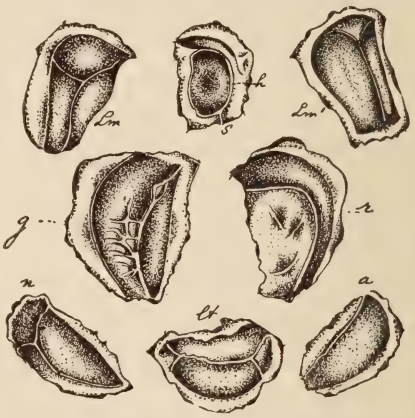


Fig. 98. Seeds. *Lm, of O. Lamarckiana,* seen from the back; *Lm'*, seen from the other side which has a sharp ridge on it; *g, O. gigas*; *r, O. rubrinervis; n, O. nanella; lt, O. lata; a, O. albida*; *s, O. scintillans,* opened and empty; *h,* the hard layer which surrounds the inner lumen.

The species which bore these characters were described and named by LINNAEUS. They were *O. biennis, L., O. muricata L.,* and *O. parviflora L.* To these were added later the well-known forms *O. suaveolens Desf.* (=*O. grandiflora Ait.*) and *O. Lamarckiana Ser.* (=*O. grandiflora Lamarck*).[1] Besides these there belong to the group in question a whole series of American forms which are little known in Europe.

[1] Although the name *O. grandiflora* has good claim to priority for both these species I do not propose to use it because it has already given rise to a great deal of confusion. See *Nederl. Kruidk. Archief.* Aug. 1895.

Later systematists have either lumped all these forms into one big species or have separated them up in different ways. When they did the former, they took *O. biennis* as a type. The other species were ranged round this as varieties. This was done for example by TORREY and GRAY in their famous *Flora of North America* and by WATSON in his monograph. This is an important point for our further discussions, as showing that a minute comparative study of the various forms points to their common origin from *O. biennis.*

SPACH however thinks differently. He separates six species of *Onagra.* Two of them include all the forms which interest us; the rest are rare and do not exist in Europe either as wild or as cultivated forms. These two species are (1) *Onagra vulgaris Spach* = *Oenothera biennis L*; but also including *O. suaveolens Desf.* and *O. Lamarckiana Ser.* and (2) *Onagra chrysantha Spach,* which is composed of *O. muricata L., O. parviflora L., O. cruciata Nutt.* and of a *Var. latifolia* with which I am not familiar.

I think it is legitimate to conclude from this that the original *Oenothera biennis* has given rise to the remaining species mainly along three lines: 1st by an increase in the size of the flowers (*Lamarckiana*), 2d by a decrease in this size (*chrysantha*) and 3d without any change in it. The other features of the flowers are closely correlated with its size and, in fact, appear in great measure to be determined by it.

The species of *Onagra* differ from one another not only in the structure of the flowers but in that of the leaves as well. Furthermore the fruits of *O. parviflora* split by 8 apical valves instead of 4, whilst *O. Lamarckiana* has an entirely different appearance. Further, less

important, distinctions are afforded by the degree of hoariness and so forth.

The following questions suggest themselves: Has *Oenothera biennis* been through a period of mutation similar to that through which *O. Lamarckiana* is going now? If it has, did it give rise to species which now exist in the same way as *O. Lamarckiana* is doing now? Have the existing forms arisen directly from it or do they owe their origin to repeated mutations? Finally does there exist anywhere at the present moment a mutable family of *O. biennis* which is perhaps giving off some of the forms which we know and others, perhaps, as well? These and other questions must for the present be set aside for future investigation to answer.

At any rate they serve to illustrate the theme of the present chapter, which is that the *Onagra*-group is precisely parallel to the group of mutations which is being produced by *O. Lamarckiana.* It is older and perhaps more extensive. But if the distinctions between species within the two groups can be shown to be of the same systematic value, the parallel between my new species and the older species of recognized position will strongly be supported by pure systematic evidence.

Now that I have foreshadowed the contents of the paragraphs that follow, let us go back to *O. Lamarckiana.*[1]

[1] *Oenothera grandiflora Ait.* = *O. suaveolens Desf.* is often confused with *Lamarckiana* either under one of these names or as *O. macrantha Hort.* The facts are as follows It was first described by Willdenow in his *Species Plantarum* (Vol. II, 1799, p. 306) but seems to have been figured before that time by L'Heritier, *Stirpes novae,* Tom. II, Plate 4. De Candolle in his *Prodromus* suggests that *O. grandiflora Ait.* and *O. suaveolens Desf.* may perhaps be different species. Desfontaines who gives no description of it in his Tableau (1st edition 1804, p. 169; 2d edition 1815, p. 195) seems to regard the two names as synonyms.

In the general Herbarium of the Museum of Natural History at Paris I found in the drawer for *O. biennis* a sheet of paper on which

First I shall give a translation of LAMARCK'S own description of the species. In order to understand this we must bear in mind that LAMARCK was not comparing it with the forms most closely related to it but with another form with very large flowers, *O. longiflora*, belonging to another subgenus. Moreover he had neither seen specimens from America, nor living plants either wild or cultivated. His description rests on dried specimens in the Paris Herbarium, which had been grown in the *Jardin du Muséum d'histoire naturelle.*

LAMARCK'S words are: Leaves entire, oval-lanceolate, petals not indentate, fruits glabrous. This species bears a general resemblance to *Oenothera longiflora* but can be distinguished from it by a number of obvious characters, in particular by its branched stem, its entire leaves and short and smooth fruits. Its stem is three to four feet high, cylindrical, almost glabrous, of a reddish brown color with numerous projecting branches. The leaves are green, spirally arranged, oval-lanceolate, glabrous on both sides and entire; the lower leaves are petiolate and slightly toothed below. The bracts are nar-

two stems of *Oenothera grandiflora Ait.* had been stuck. One of them bore this name in the handwriting of MICHAUX. At the side of the other DESFONTAINES had written *Oenothera suaveolens Hort. paris.* Somebody else had written above it *Oenothera grandiflora* and *Poiret Encycl.*, and there is written underneath it in the handwriting of SPACH: *Onagra vulgaris grandiflora Spach.*, which name, in SPACH'S Monograph (p. 353), is synonymous with *O. grandiflora Lam.* SPACH therefore, we see, did not distinguish between these two *grandifloras* although they are absolutely unlike one another.

These two specimens are identical with the form frequently cultivated in gardens under the name of *O. grandiflora Ait.* = *O. suaveolens Desf.* I have also often got it under the names of *O. macrantha Hort.* and *O. odorata Hort.* (the latter name is erroneous and is due to the French name *Enothère odorante*).

My investigations in the Herbarium at Paris have convinced me of the identity of the form I cultivate as *O. suaveolens Desf.* (*O. macrantha Hort.*) with the form described by DESFONTAINES. Both of them have flowers of the same size as those of *O. biennis.*

rower, more pointed and sessile. The flowers form a broad terminal cluster; they arise singly from the axils of the bracts but are crowded close together. The calyx is yellow, the tube somewhat longer than the four lanceolate broad-based sepals, which are terminated by a short, fat, thread-like prolongation. The four petals are oval, very large, and rounded, almost as long as the calyx-tube and tapering down to a narrow base. The fruit is a short capsule; it is cylindrical, glabrous, and truncate, square in section and is about one-third of the length of the calyx-tube.[1]

The original specimens described by LAMARCK are still in the Herbarium of the Museum of Natural History at Paris and are marked there with the same number as they are in the Dictionnaire. I have carefully compared these specimens with the plants which I have cultivated in my experimental garden and have convinced myself of the identity of the two.[2] The original specimens, however, by no means represent the mean type of the species in every respect and therefore the description does not exactly correspond to this type, particularly as regards the corolla and the fruits. The petals are obcordate but only slightly emarginate as compared with *O. longiflora*; the fruits are of the same form and size

[1] *Encyclopédie méthodique, Botanique par* LAMARCK, Tome IV. Paris, An. IV (1796), pp. 550-554. Usually cited as LAM. *Dict.*

[2] It appears that it was not LAMARCK but POIRET who wrote the section on *Oenothera* in the *Dictionnaire*. The specimens in the Herbarium bear the note *O. grandiflora* written by POIRET. In the same Herbarium there is in the case for *O. biennis*, a specimen of *Oenothera grandiflora Lam.* from the collection of Father POURRET: both plants were given to the Museum in the year 1847 by Dr. BARBIER. This plant was probably picked by POURRET in the garden of the Museum at the time of his visit to Paris in 1788. Later, SPACH made the following note on this specimen: *Onagra vulgaris grandiflora Spach,* which proves the identity of this name with *O. Lamarckiana.* This plant also agrees exactly with the form I use in my cultures.

as those of *O. biennis* and agree moreover with these in the amount of hoariness.[1]

The subgenus *Onagra,* to which *O. Lamarckiana* belongs, comprises North-American forms almost exclusively. The various forms growing wild in Europe have been imported from there. *Oenothera biennis* from Virginia about 1614, *Oenothera muricata* from Canada in 1789 by JOHN HUNNEMANN, *Oenothera suaveolens* in 1778 by JOHN FOTHERGILL.[2] The first two grow abundantly in the Netherlands, on the sand dunes which stretch along the coast, where each consists, so far as I am aware, of a single subspecies. They are widely distributed throughout Europe. *O. suaveolens* grows wild at the present time in many localities in the western parts of France.[3] The native country of *O. Lamarckiana* is unknown, but is probably Texas.[4] It only occurs wild with us when it escapes from gardens.

One of the characters of *O. Lamarckiana* is the symmetrical floral structure, which is best seen in the stamens.[5] The flowers project sideways from the stem, often almost horizontally. The stamens are inclined downwards at their base; the upper ones more than the lower ones; the upper halves being more or less erect.

[1] I refer the reader who is interested in a further discussion of the synonymy and wants a further account of the characters of these species to *Sur l'Introduction de l'Oenothera Lamarckiana dans les Pays-Bas,* in Nederlandsch Kruidkundig Archief, Aug. 1895.

[2] W. T. AITON, *Hortus Kewensis,* 2d edition, Vol. II, 1810, p. 341.

[3] GILLOT, *Soc. Bot. France,* 1893, p. 197. See also Tome III, p. 437.

[4] The strain which is now being cultivated in European gardens was introduced from Texas about 1860. See *Ber. d. deutsch. Bot. Gesellschaft,* 1905, Bd. XXIII, p. 382. (Note of 1908).

[5] H. VÖCHTING, *Ueber Zygomorphie und deren Ursachen,* in PRINGSH. Jahrb. f. wiss. Bot., Vol. XVII, 1886, p. 311. See Plate XVI, Fig. 14, in particular. For an account of geotropical curvations of *Oenothera*-flowers, see also HANSTEIN, *Beiträge zur allg. Morphologie,* IV, 3, p. 151.

VÖCHTING found that this symmetrical bending was due to gravity. He fixed branches to a clinostat and observed that the flowers opened normally but that the filaments remained straight. Neither light nor darkness had any influence on these processes. The bending of the filaments takes place just before, or during the unfolding of the flower. If, about the middle of the day on the evening of which the flower will open, we open a bud we find the filaments perfectly straight.[1]

It follows from this that the degree of bending in the filament depends on the angle which the open flower makes with the perpendicular. The smaller the angle the less the bend.

In all these respects our species behaves like *O. biennis*. On the other hand in *O. muricata* and *O. parviflora* the filaments are not bent.[2] The absence of bending in this case, however, directly depends on the fact that the flowers in these species instead of projecting sideways stand up erect. As a matter of fact, this bending is not entirely absent; I always found some signs of it even if they were only very slight ones.

§ 27. SYNOPSIS OF THE CHARACTERS OF THE NEW SPECIES.

My new species, without exception, possess the general characters of the *biennis*-group to which *O. Lamarckiana* belongs. According to WATSON's Monograph of the genus, the following are the characters of this group.[3]

[1] See the Figure on page 218.

[2] *Bull. Soc. Bot France*, T. III, p. 437.

[3] SERENO WATSON, *Revision of the Extra-tropical North American Species of the Genus Oenothera*, Proc. Amer. Acad. of Arts and Sciences, May, 13, 1873, Vol. VIII, pp. 573-618.

Plants annual or biennial, forming an erect, for the most part branched stem. Flowers yellow, buds erect, surmounted by the four tips of the calyx. Anthers linear, each inserted at its center upon filaments of equal length. Stigma formed of four or more long cylindrical parts, which are either free or more or less fused laterally. Calyx tube narrow, slightly broader at the top. Fruits sessile, oblong, tapering upwards; seeds in two rows in each loculus; the integument of the seeds too big for the kernel and therefore wrinkled.

This list, taken in conjunction with the following tables, will suffice to show that the new species belong to the group in question both morphologically and systematically. That they are more closely related to *O. Lamarckiana* than to *O. biennis, O, muricata, O. suaveolens* or the other species of this group described in systematic works, is shown, apart from their origin, by certain characters of the flowers. In the first place these are much larger than they are in the other forms; and, in the second, they have a longer style. The style raises the stigma in the bud above the tips of the anthers. When the flower opens the four stigmas expand into the form of a cross, not touching the anthers, however, as a rule. In *O. biennis* on the other hand the stigmas lie, in the bud, between the anthers and do not reach above them at the time of flowering.

This state of affairs is very important from the point of view of fertilization. In *O. biennis* this takes place in the bud because the anthers dehisce a whole day before the flower opens; though the exact time of this is of course subject to some variation. This fact obviously makes the operation of castration preliminary to crossing much more difficult, because it has to be done on very

young buds. On the other hand it facilitates self-fertilization by rendering it superfluous to do more than exclude the visits of insects. A very different state of things obtains in *Oen. Lamarckiana.* Here castration can be easily and safely effected even in large buds; but in self-fertilization the pollen has to be actually transferred. In this respect all the new species except *O. lata* and *O.*

Fig. 99. Ripe fruits shortly before drying, half natural size. *L, Oenothera Lamarckiana; R, O. rubrinervis; A, O. albida.*

brevistylis and the sterile forms behave exactly like *O. Lamarckiana* and not like *O. biennis.* The necessity of fertilizing, year after year, with my own hand every single flower from which I wanted to save seed has given me sufficient experience on this point.

In the description of the species (§§ 10-23) I made occasional reference to atavistic phenomena. For ex-

ample *O. nanella* in its earliest stages forms a few long-stalked leaves; and occasional crumples are seen in the otherwise smooth leaves of *O. laevifolia* and *O. scintillans,* etc. In this they behave like many species even in other families which reproduce in their early stages the characters of their ancestors (for example *Acacia, Ulex, Sium,* etc.).

I shall now attempt to set forth the characters of the

o *s*

Fig. 100. Ripe fruits shortly before drying; half nat. size; the bracts have not yet fallen off. *o, O. oblonga; s, O. scintillans.*

G *Lt*

Fig. 101. Ripe fruits, shortly before drying, half natural size. *G, Oenothera gigas; Lt, O. lata.*

new species in synoptic tables in order to make it easier to compare them with the characters of the older species in the section which follows. And in order to express myself as simply as possible I shall regard the character of the parent-species *O. Lamarckiana* as the normal and compare the others with it.

Further I propose to deal with the different organs

and developmental stages separately in the tables; and I shall start with the seedlings at the age (2-3 months) at which they are usually sorted out and recorded. The first table therefore gives the characters which are used in this sorting.

ANALYTICAL TABLE OF SEEDLINGS.

I. Leaves stalked.
  A. Leaves of the same breadth or broader.[1]
    1. Of the same breadth and shape, not to be distinguished as seedlings.
      a) (Fig. 48, 51, 52, 64, 65, 66, 72, 95) 1. *O. Lamarckiana.*
      b) . . . . . 2. *O. brevistylis.*
      c) . . . . . 3. *O. leptocarpa.*
    2. Broader, pointed, with many crumples.
      (Fig. 52, 63, 65, 66) . . . . . 4. *O. gigas.*
    3. Broader, rounded at the tip with very deep crumples, edge incurved.
      a) (Figs. 48, 51, 52, 91, 92, 95) . 5. *O. lata.*
      b) . . . . . 6. *O. semilata.*
  B. Leaves narrower.
    1. Broadest in the middle.
      a) very long with long stalks, with narrow veins, almost smooth (Fig. 83) . . . . . 7. *O. elliptica.*
      b) small with broad leaf-stalk and broad principal veins, very smooth, shiny, dark green (Figs. 51, 81, 82) . . . . . 8. *O. scintillans.*
    2. Of equal breadth over the greater part of their length.
      a) green.
        a) 1. Only slightly narrower, smooth without, or almost without, crumples . 9. *O. laevifolia.*
        a) 2. Very narrow with broad leaf-stalks and broad veins which often are reddish; wrinkled (Figs. 48, 53, 72, 73, 74, 95) . . 10. *O. oblonga.*

[1] "(than in *Lamarckiana*)" as also in the other analytical tables.

b) whitish.
b) 1. Crumples many, pointed, narrowing off into the stalk (Figs. 48, 72, 75, 76, 95) . . . . . 11. *O. albida.*
b) 2. Crumples few, narrowing off into the stalk, wavy, brittle, veins reddish— (Figs. 52, 68) . . . . 12. *O. rubrinervis.*
b) 3. Crumples few, scarcely narrowing off into the stalk, almost grasslike . 13. *O. sublinearis.*

II. Leaves sessile, short and broad, almost heartshaped, crumpled (Figs. 51, 52, 78, 79) 14. *O. nanella.*

The new species can best be distinguished from one another by their so-called habit. This is, as in the case of *O. Lamarckiana* itself, largely dependent on external conditions. In the first place biennial plants are as a rule naturally stronger than annual ones. The former are sometimes more than two meters high; the latter often little more than a meter. In both cases the time of sowing makes a difference; the earlier the plants come up the more time they have for their full development. The height and amount of branching of the plants are largely dependent upon the amount of sunshine they get, and on whether they are growing close together or not.

The result of this is that spurious differences, which are either indirectly connected, or not connected at all, with real specific characters, may appear in comparing cultures of related species, and obscure the real differences. On the other hand genuine differences sometimes tend to become obliterated. But if uniformity of treatment is insured, beds of my new species have a perfectly distinct and different aspect and can be recognized with certainty, even at a distance.

The following table mainly refers to annual plants in flower.

ANALYTICAL TABLE OF FLOWERING PLANTS: HEIGHT AND MODE OF BRANCHING.

I. Of the same or nearly the same height (1.5—1.8 m).
  A. Flowering over in October. Stem erect, rigid
    1. Of the same strength.
      a) Secondary stems strong, branches short, foliage lax (Fig. 55) . . . 1. *O. Lamarckiana.*
      b) Secondary stems weak, main stem branched; infrutescence lax; stem reddish, brittle, often wavy (Fig. 49, 67, 69, 70) . . . . . 2. *O. rubrinervis.*
    2. A little weaker.
      a) Leaves narrow, very much like *O. Lam.* (Fig. 56) . . . . . 3. *O. laevifolia.*
      b) Leaves broad, like *O. lata* but taller . . . . . 4. *O. semilata.*
    3. Very strong, stem stout and very erect, dense foliage, short internodes, branches short and rosette-like. Inflorescence closer and fuller . . . 5. *O. gigas.*
  B. Flowering continues till winter. Weak and drooping at that time.
    1. Much branched; flowers many; group of buds above the flowers small . . 6. *O. brevistylis.*
    2. Slightly branched; flowers rare; group of buds above the flowers very long . . . . . 7. *O. leptocarpa.*

II. Shorter (about a meter or less).
  A. Much branched.
    1. Branches pressed close to stem; the whole plant rigid. Bud-bearing zone above the flowers long . . . . . 8. *O. scintillans.*
    2. Branches projecting outwards, rigid.
      a) Main stem thick, projecting above the branches . . . . . 9. *O. albida.*
      b) Short, weak . . . . . 10. *O. elliptica.*
      c) Usually very weak . . . . . 11. *O. sublinearis.*

3. Branches weak, and so bent downwards. top of plant also weak . . . 12. *O. lata.*

B. Almost unbranched, branches in the form of rosettes, stem very thin (Fig. 50, 71) . . . . . 13. *O. oblonga.*

III. Dwarf, often flowering when only 10–20 cm. high (Fig. 45, 77) . . . . . 14. *O. nanella.*

In *Oenothera Lamarckiana* every part of the plant has a characteristic type of leaf from the seedling to the top of the inflorescence. The same is true of the new species which have arisen from it. The radical leaves of the full grown rosettes merge by imperceptible degrees into the lower leaves of the stalk. As we ascend the stem, the leaves become gradually shorter and set on smaller stalks until we reach the inflorescence, at the bottom of which, or slightly later, they become almost sessile. In the young inflorescence they extend beyond the flowers, but, later on, become relatively small compared with them. The greatest breadth of the leaf, which at the bottom of the plant is about its middle, gradually shifts, as we ascend, to its base. In describing the leaves of the different new species we must therefore compare only such as are borne on the same part of the stem.

ANALYTICAL TABLE OF THE LEAVES.

I. Of normal breadth.

A. Of normal length and form.

1. Pointed.

a) (Figs. 62, 89) . . . . . 1. *O. Lamarckiana.*

b) . . . . . 2. *O. leptocarpa.*

2. Rounded . . . . . 3. *O. brevistylis.*

B. Roundish . . . . . 4. *O. semilata.*

C. Short, sessile or with a short stalk; broad at the base; often auriculate or heart shaped 5. *O. nanella.*

II. Broader.

A. Of the same form, but very variable, teeth large, numerous, especially at the

base. Those on the stem bent downwards. (Fig. 54, 62) . . . . . 6. *O. gigas.*
B. Round, stumpy, slightly toothed, but usually with an incurved edge (Fig. 57, 58, 88, 89) . . . . . 7. *O. lata.*

III. A little narrower.
A. Green.
1. Smooth, without crumples.
a) Of normal length, flat . . . . . 8. *O. laevifolia.*
b) Small, median vein broad, whitish (Fig. 54) . . . . . 9. *O. scintillans.*
2. Uneven; radical leaves narrow with a broad vein; leaves on the stem sessile and with a broad base (Fig. 54) . . 10. *O. oblonga.*
B. Whitish.
1. Often with red veins; broadest in the middle, bracts folded longitudinally (Fig. 54) . . . . . 11. *O. rubrinervis.*
2. Sessile with a narrow base; only the lower leaves stalked (Figs. 54, 57) . 12. *O. albida.*

IV. Very narrow.
A. Lanceolate, long, often ten times as long as broad (Fig. 83) . . . . . 13. *O. elliptica.*
B. Almost linear, small (Fig. 85, 86) . . 14. *O. sublinearis.*

To turn now to the flowers; I have already stated above that their size depends largely on the strength of the plant which bears them. They exhibit both individual and partial variability and follow QUETELET's law in these respects. A very striking fact is that their size gradually diminishes during the flowering period (which lasts from July till October) and that at the end of it they sometimes sink to ⅔ or even half their original size. This is obviously determined by the exhaustion of the plant by fructification; for *O. brevistylis,* which sets practically no seed and often goes on flowering until well into November, bears large and bright flowers even at that time. The flowers are smaller on the lateral branches if the main stem is laden with fruits. But

if part, or all of this, has been cut off during early life (as is often done for the purpose of artificial fertilization) the lateral branches bear remarkably large and fine flowers.

It follows from this that those new species which are of a delicate nature will have somewhat smaller flowers.

ANALYTICAL TABLE OF FLOWERS, FRUITS AND SEEDS.

(Figs. 98–101.)

I. Flowers as large or larger, petals, on the average 3–4 cm. long (plants large).
  A. Fruits and seeds normal; buds thin; tapering to the top (Fig. 99).
    1. Calyx and fruits green, sometimes slightly reddish (Fig. 61) . . . . 1. *O. Lamarckiana*
    2. Calyx reddish, fruits striped with red, petals often more or less crumpled, broad, becoming darker as they fade 2. *O. rubrinervis.*
    3. Pale yellow; the later flowers with oval petals (Figs. 59, 60) . . . . 3. *O laevifolia.*
  B. Fruits short and thick (Fig. 101).
    1. Seeds dark brown, large and plentiful; petals very broad; buds thick . 4. *O. gigas.*
    2. Seeds large, scanty; buds fat; petals crumpled; anthers sterile (Fig. 46) . 5. *O. lata.*
    3. Almost the same, pollen fertile . . 6. *O semilata.*
  C. Fruits short and thin, flowers short-styled, ovary partly superior . . . 7. *O. brevistylis.*
  D. Fruits long and thin. Flowering does not begin until late in the summer and lasts well into the autumn . . 8. *O. leptocarpa.*

II. Flowers smaller, or very nearly as large; petals about 3 cm. long (plants short).
  A. Fruits long and thin; flowers much expanded; petals elliptical.
    a) Fig. 84 . . . . . 9. *O. elliptica.*
    b) Fig. 87 . . . . . 10. *O. sublinearis*
  B. Fruits of almost normal size.
    a) Seeds plentiful, of almost normal size. Buds often laterally twisted . . . . . 11. *O. nanella.*

b) Fruits thinner, poor in seed; flowers pale yellow, corolla less expanded. (Fig. 88, 89) . . . . . 12. *O. albida.*

C. Fruits short and thick, of half the normal size or less.

a) Flowers erect; seeds small; fruits smooth . . . . . 13. *O. scintillans*

b) Flowers projecting sideways; fruits not so stout, poor in seed . . . 14 *O. oblonga.*

The characters given in these tables are those which I have myself ordinarily employed in sorting and recording my plants. But there are also small differences which practice enables one to recognize with ease, and to employ with certainty. It is, however, almost impossible to express them in words. And the above mentioned circumstance that the degree of development of all the organs is highly correlated with the individual strength of the plant always makes descriptions appear incomplete; but, on the other hand, materially facilitates the discriminations of the living material.

§ 28. COMPARISON OF THE CHARACTERS OF THE OLD AND NEW SPECIES.

The new species which have arisen in my experimental garden from *Oenothera Lamarckiana* differ from one another in the same way as do the already known species of the *biennis*-group. I shall now endeavor to prove this important generalization by a detailed comparison of the two groups. Unfortunately the difficulty of giving this proof is considerably enhanced by the incompleteness of the descriptions which have been given in the literature. The diagnoses are usually short, often based on single herbarium specimens about which we have no means of knowing in what characters they repre-

sent the mean of the type and in what they deviate from it, and if so, to what extent. There is practically no information about the seedlings; and this would have been particularly valuable in this case. And so forth.

These gaps in the literature can of course best be filled up by growing the species in question; and for many years I have cultivated the forms which grow wild with us and some other ones, on a large scale and under different conditions. In 1895 I procured in exchange from the botanical gardens all the available samples of seed of the subgenus *Onagra* and sowed as many of these as I could manage. And since then I have taken every opportunity that offered, of procuring *Onagra*-seeds.

I am, of course, most familiar with the forms which grow wild with us, *O. muricata* and *O. biennis*; but I only possess one form of each of these.[1] I am familiar with *O. suaveolens* which is widely distributed over France and have two subspecies of it; with *O. hirsutissima* (*O. biennis hirsutissima* TORREY *and* GRAY); with *O. parviflora L.* and *O. cruciata Nutt.*; and with some others. I am only acquainted with figures or herbarium specimens of *O. spectabilis Spach* (*O. corymbosa*), *O. elata Kunth, O. media Link, O. erosa Lehm.*, etc. But they are intermediate in character, so far as it is possible to judge, between the two species mentioned first; in fact they bridge over the gap between these two to a large extent.

For these reasons I shall confine myself almost entirely to the comparison of the new species with *O. biennis, O. muricata, O. Lamarckiana, O. cruciata* and

[1] Probably the types, used by LINNAEUS for his descriptions. Compare Note on page 431. (1908.)

O. suaveolens. This will be sufficient to show that the differences between the former are greater than those between the latter. A study of the other old species would obviously only serve to bear out this conclusion.

Let us begin with the seedlings. They fall into two groups. *O. biennis* and *O. Lamarckiana* have broad leaves (Fig. 102 A), *O. muricata, O. cruciata* and *O. suaveolens* narrow ones (Fig. 102 B).

These differences can be seen particularly well in very young rosettes; but when the leaves begin to grow quickly as they do in June they all become longer and their distinguishing feature, therefore, less striking (Fig. 103),

A B

Fig. 102. Seedlings. A, of *Oenothera biennis L.*; B, of *O. muricata L.*, two months old.

only however to become quite clear again later on. I have often grown rosettes of various new and old species in rows, close to one another, in order to compare 10-20 or more individuals of the same age and under the same conditions. *O muricata* and *O. scintillans* differ most widely from the normal in the narrowness of their leaves; in both of them the leaves are smooth and shiny; in the former however they are pale green and long, in the latter dark green and short. *O. rubrinervis, O. suaveolens* and *O. hirsutissima* have wavy crumples and

pale leaves. They look very much alike when young, but the first of them can be distinguished earlier and with greater certainty from its neighbors (in hybrid crops for example). Rosettes of *O. gigas* are much larger and stronger than those of *O. Lamarckiana*; these are about as vigorous as *O. biennis,* but their leaves are not smooth like those of *O. biennis* but uneven. *O. elliptica* is often scarcely distinguishable from *O. cruciata; O. sublinearis*

Fig. 103. Full grown leaves of young rosettes in June at the age of 3 months. B, *O. biennis*; M, *O. muricata*; S, *O. suaveolens.*

has the narrowest leaves of the whole group. Between this latter and *O. gigas* the various old and new species form a perfect series of transitional forms.

Although single individuals or their figures convey only a very imperfect impression of a species, I invite the reader to compare Figs. 102 and 103 with those, which have already been given, of rosettes and leaves.

First with the groups of leaves from rosettes in June (Fig. 52, p. 293 and Fig. 53, p. 294); and then with the rosettes of *O. gigas* (Fig. 63, p. 324), *O. lata* (Fig. 92, p. 412), *O. scintillans* (Fig. 82, p. 383), *O. oblonga* (Fig. 74, p. 344) and so forth.

The radical leaves of the full grown rosettes and the leaves on the stem behave in the same way. Those of *O. biennis* and *O. Lamarckiana* hardly differ at all in

Fig. 104. Radical leaves of full grown rosettes. B, of *Oenothera biennis*; L, of *O. Lamarckiana*. The spots on the leaves are brown in life.

form (Fig. 104 B and L). Those of the former are smooth with few crumples, with red main nerves, and often a number of scattered brown spots; the latter are very much wrinkled, without red pigment or at most with no more than isolated red spots. In form, *O. gigas* differs somewhat more (Fig. 62 on page 323) and *O. lata* more still (Fig. 58, p. 311, and Fig. 89, p. 405).

At Fig. 105, p. 460 will be seen a group of stem leaves for comparison with the corresponding ones in Fig. 54 on page 295. The differences are obviously of the same order. In the case of *O. cruciata* and *O. muricata* (Fig. 105, *p* and *m*) they are most pronounced; and still more so in *O. elliptica* and *O. sublinearis,* which are not included in Fig. 54.

With regard to "habit" the majority of the older species do not differ much from one another. *O. muricata* has usually stronger lateral branches than *O. biennis*; *O. Lamarckiana* has a longer spike than either. *O. cruciata* is shorter than *O. biennis,* which, however, *O. suaveolens* and *O. hirsutissima* very much resemble, though they are less robust. All these comparisons are of course made between plants under similar conditions of cultivation. Under such conditions *O. rubrinervis, O. gigas, O. laevifolia* and *O. brevistylis* do not differ so much from *Lamarckiana* as do the shorter forms which have an entirely different habit. Amongst these *O. lata* is broad, close and compact whilst *O. oblonga* and *O. scintillans* with their narrow leaves have a rigid and thin stem which branches only slightly or not at all.

The glaucous color of *O. muricata* is characteristic of this species; the green of *O. albida* is paler than, and that of *O. rubrinervis* about the same as that of *O. suaveolens* and *O. hirsutissima.* These four forms are very much alike, apart from their flowers and fruits.

With regard to the flowers the differences are much greater between the older species than they are between the new ones. The flowers are small in *O. muricata, O. parviflora* and *O. cruciata*; medium in *O. biennis, O. suaveolens* and *O. hirsutissima,* and very large in *O. Lamarckiana.* In the first group they are erect, and their

stamens therefore not bent (see. p. 444) ; in the two latter groups they project outwards and the androecium is modified correspondingly. In *Lamarckiana* the stigma ex-

Fig. 105. Stem-leaves of *Oenothera biennis* (*b*) ; *O. suaveolens* (*s*) ; *O. hirsutissima* (*h*) ; *O. cruciata* (*p*) ; *O. muricata* (*m*) ; to be compared with Fig 54 on p. 295.

tends beyond the anthers; it reaches the same level in the other forms.

In all these and other details the new species have the flowers of *Lamarckiana.* But during the last two years my mutants have overstepped even this limit; one having appeared with *biennis*-flowers and one with *muricata*-flowers, not however in pure but in crossed strains.

A curious form must be mentioned here, *Oenothera cruciata Nuttall* which is described by some systematists as a species, but regarded by others as a variety of *O. parviflora,* from which it differs by its small linear petals but in no other respect. It is therefore more closely allied to *O. parviflora* than any two of my new species are to one another.

Lastly let us look at the fruits. The older species resemble each other with the exception of *O. parviflora,* in which the capsule is described as opening by eight valves instead of four. The other alleged differences such as cylindrical or conical form, greater or less degree of hoariness, length and thickness, etc. are subject to a very great extent to individual fluctuations and do not seem to constitute differences of specific rank.

On the other hand it is just in the characters of the fruits and seeds that the new species differ most amongst one another, as the table on page 453 and Figures 98 (group of seeds, p. 438) and 99-101 (fruits, pp. 446-447) clearly show.

We can sum up by saying that the known systematic species of the subgenus *Onagra* differ from one another in essentially the same way as do the forms which have arisen from *O. Lamarckiana.* The two groups are precisely analogous. The relation between the group of *Onagra*-species and *O. biennis* is the same as that between the group of *Lamarckiana*-mutants and *Oenothera Lamarckiana* itself.

IV. ON THE LATENT CAPACITY FOR MUTATION.

§ 29. REPEATED MUTATIONS ARE THE RESULT OF THE SAME INNER CAUSES.

Hitherto I have confined myself to a mere description of the phenomena of mutation in the genus *Oenothera* such as I have directly observed them. Our task now is to form some idea of the causes of these phenomena.

The attempt to deal with this problem is not only a perfectly legitimate one but the reader would be justified in complaining that my work were incomplete if I did not attempt to deal with it.

The solution of this problem must, however, be sought among the facts themselves. And for this purpose I shall divide my argument into two parts. The causes which can be dealt with most easily are, naturally, those which operated throughout my experiment, that is the internal and external causes of each of the several mutations. But to provide an answer to the questions: what is the cause of the whole phenomenon, and to what is the initiation of the mutation period due? is a task of a very different nature. And I propose to postpone this to the last section of this chapter.

The facts, summarized in this and the previous section, of the repeated reappearance of the mutations observed in my cultures evidently admit of one explanation only, viz., that the potentiality for each mutation is present in a latent condition in the apparently normal individuals in my cultures.

Let us take as an example the *Lamarckiana*-family (p. 224), of which I have grown a great number of successive generations. The first sowing gave two mutations (*lata* and *nanella*); the following generation gave them again, and one other besides. The seeds for this second sowing were gathered from 6 seed-parents which had flowered far away from other *Oenotheras* and therefore can only have been fertilized by one another. They were obviously chosen without any indication whether they would be more likely to produce mutations than the remaining individuals of the first generation. That these six seed-parents reproduced the same mutations as their parents proves that there existed in them some heritable character in a latent condition.

The same is true of subsequent generations and of the other families in my cultures. Each time the same mutations arose from apparently normal individuals. The capacity for giving rise to these must therefore have been inherited in the latent condition.

If a latent capacity of this kind is not assumed the following three facts become absolutely inexplicable.

First, the circumstance that the same mutation appears in the same crop in two or more of several individuals, whether the crop arises from the seeds of one or several seed parents.

Secondly, the oft cited fact (Part II, p. 272 etc.) that the appearance of mutations seems to depend almost

exclusively on the extensiveness of the crop. Whenever I had the opportunity of sowing on a large scale, either with seeds from the field at Hilversum (1889) or, in my own families, with the seeds of a few seed parents, especially in the year 1895 (p. 224 and p. 262), a large number of mutations appeared. Their rarity in other years and cultures can therefore only be attributed to the small scale on which the sowings were made; for on a few square meters we cannot expect to get many mutations if the seeds are not sown very close and the crops are not examined every day.

Thirdly, the small number of the different mutations which appeared. By no means does every conceivable deviation occur. Thus there arose no white flowers, no glabrous or unbranched individuals, no linear petals,[1] no trace of petalomany or apetaly and so forth. Even of the two new species which were found in the field at Hilversum, *O. brevistylis* and *O. laevifolia,* not a single example occurred in my cultures.

We are led to the same conclusion by a consideration of the more or less incompletely developed individuals of the new species which sometimes seem to constitute transitional forms. For these arise in my cultures not *before* the mutants, but simultaneously or more commonly only after them. Each mutation is as completely developed when it first appears as afterwards. When a mutation is grown through many generations and on a very large scale its various representatives conform to exactly the same type. I possess photographs and descriptions of my mutations from the first year of their appearance and find that nothing has been added to, or

[1] *"Forma cruciata"* as found in *Oenothera cruciata Nutt.* and some others.

taken away from, their type. I have often had *lata*-plants from two or three sources, e. g., the 1st, 2d and 5th generations, growing side by side in my garden; they were quite indistinguishable from one another.

Intermediate forms seem to be associated more with some mutations than with others. Rarest with *O. nanella,* they are commonest with *O. laevifolia.* Sometimes the intermediate forms repeat the new type of their species more or less completely in the lateral branches which arise from the axils of the rosette leaves (as for example an *O. laevifolia* which exhibited excessive crumpling on the leaves borne on the main stem). In this case they may be regarded as individuals in which the typical character of the species is more or less latent at first.

Thus these apparent transitional forms are not the steps by means of which the new species has attained its full development. They are rather the imperfect copies of a perfect picture which already exists. They are, in a word, the extreme variants of the perfectly constant new type (see §§ 24 and 25).

It is in this very respect that the newly formed species behave in a diametrically opposite way to the races built up by the accumulation of fluctuating characters (Part I, § 7, p. 71); and it is this fact which justifies their title to specific rank.

The general conclusion of this argument is:

At the beginning of my observations, in the year 1886, the characters of the new species, which appeared later in my cultures, were already present in the plants in the field at Hilversum in a latent condition. They remained in that condition for many generations, both there and in my cultures, and only appeared from time to time, especially in large sowings.

I regard this conclusion as thoroughly proved in the case of the commoner species which appear in measurable proportions (e. g., 1% or 0.1%). Whether or no it also holds good for the rarer ones or for those which did not appear till late must be regarded as of no concern for the present.

But if the existence of this capacity in a latent condition in 1886 is demonstrated by my cultures, it follows that all or most of these new species existed in a latent condition before that date.

This latent capacity to mutate, i. e., to produce a series of definite and identical mutations, is therefore a heritable character in my *Oenothera Lamarckiana*. The particular factor for every given mutation must obviously exist separately. And it must be supposed that the various mutations, although they belong to the same group or period, are nevertheless independent of one another.

As far as observation goes, this potentiality is always inherited by all individuals. Of course many sowings have given no mutants, and in other sowings certain mutants have been lacking. But this may always have been the result of the smallness of the scale on which the experiment was carried out (whether this was because the available quantity of seed was insufficient or that a small culture was all that was necessary for the immediate object of the experiment). In larger crops all the commoner mutants appeared as a rule. For large cultures like these the seeds of four or even 10-20 seed-parents were needed. In these cases I have always sown the seeds from each parent separately and it has never happened that no mutants appeared amongst the progeny

of any single seed-parent. If some mutants were absent, others were more numerous to make up for it.

The power to mutate is also inherited by the new species. We have already seen several examples of this in § 8 and later in §§ 10-23. For instance *O. scintillans* is very mutable: it produces pretty regularly 10-20% *oblonga;* about ⅔% *O. lata* and about ⅓% *O. nanella* (p. 244). *O. oblonga, O. nanella, O. leptocarpa* and others gave also rise pretty regularly to the other mutational forms in proportions not very different from those in which they are produced by *O. Lamarckiana* itself (§ 8). And the same is true of crosses, for example between *O. lata* and *O. nanella, O. rubrinervis* and *O. nanella* and so forth.

Therefore, when a character passes from its latent to its active condition, all or apparently all of the other characters latent in it remain so. They are not lost in the process.

The question arises: are they ever lost?

O. brevistylis and *O. laevifolia* seem to afford an answer to this question. They grew in 1887 in the field at Hilversum, they are not known anywhere else and, what is more to the point, they have not been observed as mutants a single time in my cultures, even in cultures of many thousands of individuals. It is therefore possible that they no longer exist in my species in a latent condition.

It is, of course, possible that my plants may not have descended from the same individual ancestors as those from which these two species arose. So that my observations do not afford a definite proof that the latent characters of these species have been lost. But, inasmuch as the whole lot of the *Oenotheras* in the wild locality has

only sprung from a few individuals, the conclusion that they may have been lost seems to me very probable.

It is hardly possible to discover whether single plants in my cultures may sometimes lose the power of giving rise to particular mutations. The negative results of the experiments do not enable us to decide. Far more extensive cultures would be necessary to answer this question definitely by experiment.

Meanwhile I incline to the view that the separate latent characters, which become visible by mutation, may be lost sooner or later.

§ 30. THE LATENT INHERITANCE OF OTHER CHARACTERS IN OENOTHERA LAMARCKIANA.

The foregoing argument has led us to regard the capacity for producing mutations as a latent heritable property. The characters of the new species exist potentially in the parent species but remain invisible until they are called into active existence by definite external causes.[1]

That this hypothesis bears strongly on the theory of mutation and on our whole conception of the nature of heritable characters is evident.[2]

For this reason, I have been trying for many years to render the inheritance of latent characters accessible to experimental study, not only in *Oenothera* but elsewhere. The best material for this work seemed to be afforded by monstrosities or teratological phenomena, which used to be looked upon as something fortuitous

[1] Variabilité et Mutabilité, *Rapport du Congrès international de botanique,* Oct. 1900, Paris, p.1.

[2] See *Intracellulare Pangenesis,* p. 16, and the second volume of this work.

but are now generally regarded as visible manifestations of a latent heritable potentiality.

In the members of certain families, (which may be large or small) the deviations in question become visible so often, that the presumption in favor of a common internal cause becomes very strong. On the other hand the monstrous individuals are so frequently separated from one another in pedigrees by perfectly normal ones that the cause, if it is a continuous one, that is, if it is handed on from one generation to another, must be inoperative most of the time. Finally the appearance, or non-appearance, of the monstrosity in particular individuals is dependent on external influences and mainly on nutritional conditions. This latter fact alone seems to me sufficient to prove their presence, and consequently their inheritance, in a latent state.

Monstrosities are much more favorable material for this purpose than mutations. For they are accessible to everybody, and dependent for their appearance and degree of development on their environment in ways which are easily investigated. Except for hybrids, they afford the best material for studying and elucidating the general principles of latent characters.

Monstrosities differ from mutations in that their appearance is partial: by this I mean that they do not affect all the homologous organs of the same plant but only some and usually very few of them; whereas the mutations described in this part are absolutely individual. Monstrosities need, by no means, be monstrous. The appellation monstrosity is a very unfortunate one; because, in other species many of these teratological sports are quite normal characters.[1] As an example I might

[1] *Monstruosités taxinomiques*, as they are called by De Candolle.

quote the pitchers or ascidia, which are analogous to the peltate leaves. It is true that the pitchers often have the form of a cornet or pocket and this restricts the assimilatory capacity of the leaf; but that only depends on the form of the normal leaf in the species in question. If the latter is auriculate, the pitchers can be quite or nearly flat, and form perfectly typical peltate leaves; for example a pitcher-forming *Pelargonium zonale* which I have had in cultivation for years and have propagated by cuttings, gives rise, every year, to a number of such peltate leaves especially on short shoots. Similarly the first leaves of the twigs of *Tilia parviflora,* when changed into ascidia, are almost absolutely flat (Fig. 106 C).

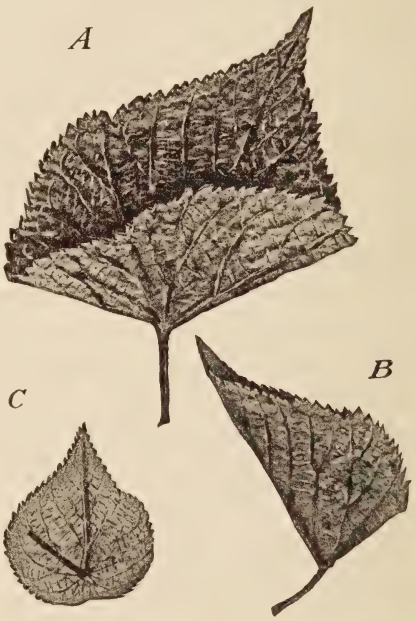


Fig. 106. *Tilia parviflora.* The formation of pitchers from leaves. A, B, ordinary ascidia; C, a peltate leaf ("flat pitcher") seen from below.

I ought to say that my conclusions on the mode of inheritance of monstrosities are chiefly based on species of plants other than *Oenothera.* They have partly been dealt with already,[1] and partly will be described in the second volume of this work.

[1] *Ueber die Erblichkeit der Zwangsdrehungen,* Ber. d. d. bot. Gesellsch., 1889, Vol. VII, p. 291; *Eine Methode Zwangsdrehungen*

But these results agree so closely with the facts related here, that there can be little doubt that my general conclusion applies to *Oenothera* as well.

I have only carried out a few direct experiments bearing on the inheritance of the abnormalities in *Oenothera Lamarckiana* itself. They relate to tricotyly and variegated leaves, and will be described in subsequent sections. I have however collected a fair number of observations which favor the argument for this inheritance of latency. A series of abnormalities have occurred in the plants in the field at Hilversum, as well as in my own cultures; some of them seldom, some of them often; but all of them in such a way as to leave no doubt as to their heritability.[1]

The only exception to this is afforded by the cases of virescence, which changes the different parts of the flowers into small green bracts. I never found it on the *Oenotheras* at Hilversum, and only on one example in my own cultures. This was a biennial dwarf which flowered in the summer of 1890, and came very near bearing no seed at all on account of this abnormality. I regard this malformation as due to the attack of some

aufzusuchen, ibid., 1894, Vol. XII, p. 25; *Ueber halbe Galton-Curven, ibid.*, 1894, Vol. XII, p. 197; *Monographie der Zwangsdrehungen* in Pringsh. Jahrb. f. wiss. Bot., Vol. XXIII, p. 14 and *Over de erfelykheid van fasciatiën,* Kruidkundig Jaarboek, Gent, 1894, IV Jaargang, p. 72.

[1] For the inheritance of monstrosities see: *Erfelyke Monstrositeiten,* Kruidkundig Jaarboek Dodonaea, 1897, p. 62; *Over de erfelykheid van Synfisen, ibid.*, 1895, p. 129; *Sur la périodicité des anomalies dans les plantes monstrueuses,* Archiv. Néerl. d. Sc. exactes et nat., Serie II, Tome III, p. 371; *Ueber die Abhängigkeit der Fasciation vom Alter bei zweijährigen Pflanzen,* Botan. Centralbl., Vol. 77, 1899; *On Biastrepsis in its Relation to Cultivation,* Annals of Botany, 1899; Vol. XIII, No. 51, p. 395; *Sur la culture des monstruosités,* Comptes rendus de l'Acad. d. Sc., Paris, Janv. 1899; *Sur la culture des fasciations des espèces annuelles et bisannuelles*; Revue générale de Botanique, T. XI, 1899, p. 136; *Ernährung und Zuchtwahl,* Biol. Centralblat, Bd. XX, No. 6, 1900, p. 193.

disease, analogous to those cases in which parasites have been observed as the causes of virescence.[1]

Monstrosities often differ from ordinary individual variations in the fact that they are deviations on one side only of the type of the species, whilst the latter deviate from both sides of the mean. In this way we get, when we have a sufficient number of instances of the same monstrosity in a given species, the socalled half-Galton

Fig. 107. *Oenothera Lamarckiana.* Fruit in the axil of a deeply split double leaf; the flower from which this fruit arose had the double number of sepals and petals and stamens as a normal flower, and was elongate in transverse section.

curves.[2] Polymerous flowers, 5-9 partite fruits, split stigmas and even fasciation, all illustrate the same law.[3] But the majority of monstrosities are much too rare to

[1] *Een epidemie van vergroeningen,* Kruidkundig Jaarboek, Gent, T. VIII, 1896, p. 66.

[2] *Berichte d. deutsch. Bot. Gesellsch.,* Bd. XII, 1894, p. 197-207, with Plate X.

[3] See *Sur les courbes Galtoniennes des monstruosités,* Bull. Scientif. de la France et de la Belgique publié par A. Giard, T. XXVII, p. 396, Avril 1896.

afford material for statistics of this kind unless we breed them for the purpose. I shall give an account of some isolated observations which will, I hope, incite others to further investigation in this field.

In PENZIG's excellent work on Teratology (Vol. I, p. 481) the whole genus *Oenothera* takes up only about half a page. Our *O. Lamarckiana* is not mentioned there and of course no monstrosities of it are described. The account of the abnormalities of *O. biennis,* however, is important from our point of view. This plant exhibits an extraordinary tendency to fasciation and often gives rise to pentamerous flowers and 5-9 partite fruits. I can confirm these statements from numerous observations of my own; I also found the number of stigmas varying in the same way as in *Lamarckiana.* CLOS cites a pistil divided into seven in *O. campylocalyx* (ibid.), and synanthy in *Oenothera* has been mentioned by MASTERS (see also Fig. 107).

Just as in *O. biennis,* the chief constituents of the monstrosities presented by the *Oenotheras* growing in the locality near Hilversum and by the families derived from them in my cultures, are fasciations, pentamerous and polymerous flowers, 5-9 partite fruits, and an increased number of stigmas. These, together with variegation of leaves and tricotyly in seedlings, which occur in other *Oenotheras* as well, are the common abnormalities; the rest, in my experience, are relatively rare. I shall therefore divide the various instances into two groups, the common and the rare ones.

The rare monstrosities were tolerably well represented in the locality at Hilversum, as compared with other wild plants. This was one of the causes of the lively impression which the great degree of variability

of this plant made on me at first. I was at first inclined to regard this phenomenon as local, like the actual mutations, but had no opportunity to institute an investigation of the matter. Perhaps other observers in other places will be able to fill up these gaps. The chief point for my purpose is the proof that a high degree of heritable variability was actually in existence in the plants in the field at Hilversum.

Tricotyly.[1] Tricotylous seedlings are fairly abundant in my cultures; hemitricotyly, which simply consists in the splitting of one of the cotyledons, is somewhat rarer. I have only recorded these two abnormalities occasionally, as compared with the others, because I regarded them as of little importance at first. The following summary of the cases noted will however give data as to their occurrence and frequency in the different families.

I have started three experiments on the inheritance of these abnormalities by sowing seeds of tricotylous plants in three different families, of *O. nanella, O. laevifolia* and *O. rubrinervis*: in the latter only, however, was the experiment continued through subsequent generations.

In the following summary the years refer to the seedlings and not to the parent plants of the preceding harvest.

In 1887 I got tricotyls from seeds collected at Hilversum; one of them grew up as an *O. lata,* but set no seed.

In 1890 I found one tricotylous seedling in the chief strain of the *Lamarckiana*-family (p. 224), and in a crop of one of its *nanella*-subfamilies: the latter grew up as a dwarf.

[1] See also the second volume.

In 1890 I got two tricotyls in the *Lacvifolia*-family (p. 273). In the spring of 1892 I sowed the seeds of the previous harvest on a large scale in the greenhouse of my laboratory. I searched for the tricotyls amongst the many thousands of seedlings, and planted them out in pots in May. There were 71 of them. Of these, 63 set seed in the same year; the seed of each plant was harvested separately and sown. In this crop I counted (March 1893) the tricotyls in 100-200 seedlings for every seed-parent. Altogether I looked through over 13,000 seedlings, and found amongst them about 1% tricotyls on the average. The proportions amongst the individual seed-parents varied between 0 and 2%; only five contained more; in these the proportions of tricotyls were 2.5—2.7—3.3—3.4 and 3.8%. Occasional hemitricotyls were discovered in this extensive experiment, and a single syncotyl. Nothing was transplanted from this crop.

I found a tricotylous plant of *O. nanella* in 1889, when *O. nanella* first appeared; in 1892 I also found three tricotyls in this race, which was well established by this time: they all remained dwarf, and set seed. In April 1893 these seeds gave four tricotyls in 800 seedlings, i. e., 0.5%, and one hemitricotyl besides. The tricotyls grew up as dwarfs; the hemitricotyl was not planted out.

In 1890 I found one tricotyl in the sowing of the *lata*-family of that year (p. 288).

In 1890 I also found one hemitricotyl in the *rubrinervis*-family (p. 273), a single tricotyl in 1891, and numerous tricotyls in the larger crops that were raised in 1892. From these latter I have since formed a tricotylous subfamily which I still cultivate, without, however, being able to increase the percentage of tricotyls to a better

amount. In 1892 I had, besides 20 tricotyls, 6 hemitricotyls which however I did not cultivate further. The seeds of each of the former was harvested separately and sown; the best of them gave 2.6—2.8% tricotyls, but the majority less than 1.5%. The proportion in 8000 seedlings was 0.7%; there were also 7 hemitricotyls and 2 syncotyls.

In 1893 I planted out 70 seedlings derived from five seed-parents which had given from 1.5 to 2.8% tricotyls. In 1894, however, they yielded a harvest in which the percentage was very low, having sunk, in the case of the best seed-parents, to 1%. I planted out about 90 of the best seedlings, with a view to obtaining seed from them. Besides the above mentioned tricotyls in the crop of 1894, I found several hemitricotyls and a single tetracotyl; also a considerable number of syncotyls and one amphisyncotyl or seedling with the cotyledons fused together on both sides.

This brief *résumé* suffices to show that tricotyly is heritable and that, in my families, it is transmitted from generation to generation even through plants with normal cotyledons, i. e., in a latent state.

Fasciation. Split and fasciated stems occur almost every year in my *Oenothera Lamarckiana.*[1] The abnormality usually occurs in the axis of the inflorescence; very rarely lower down in the stem or in the rosette. Fasciated plants occurred in all my families with a few inconsiderable exceptions; but, as far as possible I never chose them as seed-parents.

The "split stem" is, so to speak, the lowest stage in the development of this abnormality, and, consequently,

[1] *Over de erfelykheid van fasciatiën,* in Botanisch Jaarboek Dodonaea VI, 1894, pp. 92 and 95.

the commonest. In the first years of my observations in the field I made careful notes on the mode of fasciation. There were 20 cases. Of these 14 had split stems (of which one was split twice); 5 formed narrow "bands," and in only one of them was the top of the stem really broad. These figures are sufficient to show that the distribution of the frequencies of the various degrees of development of this abnormality will form a half Galton-curve.

I first found fasciations in the field at Hilversum 1886, in a flowering plant and in a dead one of the previous year (1885). I found them again in 1887, 1888, 1889, 1892 and 1893—altogether 15 cases, which were all found in one and the same corner of the field. In 1894 the fasciations were much more numerous and scattered over the whole field; I myself observed six cases; further ones were observed by others. I observed two cases of fasciation in 1888 in a garden which I had then at Hilversum: one was a plant, which I had raised from a seed which had given rise to a tricotyl in 1887, and had a stem which split twice successively; the other was a case of fasciation of a three-year-old plant which was planted as a rosette in the garden in 1887.

In 1894 I found an example of *O. brevistylis* with a narrow fasciation and a case in *O. laevifolia* was also brought to me.

In my cultures the following cases occurred. I had three cases in the *Lamarckiana*-family (p. 224) in two annual dwarfs in 1888 and 1890 respectively; neither of them were grown to maturity. In 1889 there occurred in this family a biennial plant of *O. lata* which bore two split lateral twigs. Fasciation also occurred in the *lata*-family itself (p. 285), but not until the third generation

in the year 1894 in which three of the sixteen individuals that were grown showed signs of splitting in the quite young rosettes; two of these developed strong and tall flowering stems. The fasciation repeated itself, here and there, on these plants.

In my later cultures (1895-1900) fasciation gradually came to show a predilection, so to speak, for two distinct periods on the life of the plant. First for the seedling stage. In this case the axis divides either above the cotyledons, or above the first two leaves. There arise

Fig. 108. *Oenothera Lamarckiana.* A double rosette of radical leaves at the beginning of July. The cotyledons are still on.

in this way two rosettes, whose leaves intertwine because of the closeness of the two axes to one another. In the plant figured in Fig. 108 I have bent the two axes apart and separated the two groups of leaves as much as possible before photographing it, in order to make the figure clearer. When a plant like this grows up it usually has two equally strong stems which attain the same height and begin to flower at the same time. I have only arti-

ficially fertilized such plants when it happened to be necessary to record the progeny of all the plants on the bed on which it stood. Otherwise I have suppressed them, so as not to load the cultures with plants of this inconvenient form.

Double rosettes of the sort figured have appeared almost every year since the beginning of my experiment and very often in large numbers. I found most of them in *O. Lamarckiana,* but also in *O. lata, O. nanella, O. hirtella,* etc.

The second period of the life of the plant in which fasciations are commonest occurs in autumn. If we allow the main stem to go on flowering till autumn its top often broadens out.

But most of the plants in my cultures have stopped flowering by that time. Those which have been recorded and are not wanted for other reasons are weeded out, seed plants are decapitated, and plants fertilized by insects are so heavily laden with fruits that flowering ceases of its own accord. But *O. brevistylis* is very suitable in this respect, because it practically bears no fruit and sets no seed; a character by which it is easily recognizable even when flowering is over. I have often allowed a whole bed of this species to go on flowering into November; with the result that the top of many of the plants began to broaden out either in September or October, and so quickly that, in a very few weeks, it attains a breadth of 1-2 cm. The fan-shaped tops of the stems were often as broad as they were long. As to their frequency, I had, for example, in 1898, 20 fasciated individuals in a bed of 49 flowering plants of *O. brevistylis*; that is about 40%; and in another culture of the same species 63 fasciated and 11 not; that is about 70%.

Other new and old species were also much subject to fasciation. For example in October 1899 they were particularly numerous in *O. hirtella* and some of its hybrids; many occurred amongst *O. lata* and *O. albida* in 1897; and amongst *O. nanella* in 1895. In one culture of *O. muricata* in 1896 there were as many as 80% fasciated individuals; and in the cross *O. muricata* × *O. biennis* 30% in 1896 and 25% in 1898; and so forth.

These and other observations, not worth printing, made in the garden and the field, seem to me to warrant the conclusion that the capacity to produce fasciations under suitable circumstances is heritable in a latent condition in the genus *Oenothera* or at least in the group of the *biennis*-species (subgenus *Onagra*).

Variegation of leaves. I only very seldom found plants with yellow edged leaves—the first time was in 1887; otherwise the variegated leaves were streaked in the ordinary way. I found two of these at Hilversum in 1887 and two again in 1893; I sowed the seeds of the former and got a single variegated plant amongst many green ones in 1888. Some seeds collected at Hilversum in 1888 gave one annual variegated plant.

This abnormality also appeared in my cultures from time to time. For example in the *lata*-family in 1888, 1890 and 1899; in the *laevifolia*-family in 1889 (6 examples), 1891, 1894 and 1899. In the *rubrinervis*-family in 1893 and 1894, in *O. nanella* in 1899 and amongst the *scintillans* of 1890.

The *Lamarckiana*-family gave two in 1888 and two in 1890; the first two were annual and set seed, from which I got a fair number of beautifully variegated rosettes in the following year 1889.

In the *rubrinervis*-family there were occasional cases

of an absolutely yellow seedling. These seedlings apparently contain no chlorophyl and, therefore, die after the unfolding of the cotyledonary leaves. It is worth while going into this case a little more closely. Of the tricotylous *rubrinervis*-plants whose seeds had been collected separately in 1892 there were several which gave rise to occasional yellow seedlings. One parent plant was particularly fertile in this respect. It gave rise to 498 seedlings of which 95 were absolutely yellow and 3 had variegated cotyledons. The rest were pure green; these grew well, whilst the yellow ones died young. The proportion of yellow and variegated individuals was therefore 20%: and these abnormal seedlings soon perished. Of the green ones I kept 64, some of them till they ripened their fruits, but none of them showed any signs of variegation.

Inasmuch as variegated plants were never chosen as seed-parents (except in special experiments devoted to that character) and were usually destroyed before they flowered, it follows from these observations that this abnormality is not only heritable but is maintained in the various families in a latent state from generation to generation.

Variegated plants occurred from time to time in other cultures than those of *O. Lamarckiana* itself, as I have already stated. They also occurred amongst the result of crosses between *O. Lamarckiana* and its subspecies, and between this and the older species. But the details of these observations are not worth printing.

Polymery in the flowers has not been a rare phenomenon at Hilversum during my acquaintance with the spot. Whenever I examined a large number of flowers I usually found at least one polymerous one. This was also the case in my cultures. In the first years of my

experiments I recorded about 30 polymerous flowers partly in the field and partly in my *laevifolia*-family. Below is a summary of these cases, giving also the date and place or family in which they occurred. The numbers of stigmas is noted separately (N), but the number of divisions of the fruit (O) have been omitted in some cases.

NUMBER	FORMULA	DATE	LOCALITY
1	$K_4C_5S_8N_5O_4$	1887	Hilversum.
1	$K_4C_5S_8N_6O_4$	1887	"
1	$K_4C_5S_9$	1894	*laevifolia.*
1	$K_4C_5S_{10}N_6O_4$	1888	Hilversum.
1	$K_4C_6S_{10}N_8$	1887	*laevifolia.*
1	$K_4C_{4\frac{1}{2}}S_8N_5O_5$	"	Hilversum.
1	$K_4C_{4\frac{1}{2}}S_{10}N_8O_5$	"	"
1	$K_5C_5S_9N_7O_5$	"	"
1	$K_5C_5S_{10}N_4O_5$	"	"
3	$K_5C_5S_{10}N_5O_5$	"	"
1	$K_5C_5S_{10}N_5O_5$.	1888	From seeds from Hilversum.
2	$K_5C_5S_{10}$	1886, 1887	Hilversum.
1	$K_5C_5S_{10}$	1890	*laevifolia.*
4	$K_5C_5S_{10}N_6O_5$	1887	Hilversum.
1	$K_5C_5S_{10}N_6O_5$	1894	*laevifolia.*
4	$K_5C_5S_{10}N_7O_5$	1887	Hilversum.
1	$K_6C_{4\frac{1}{2}}S_{10}N_8O_6$	"	"
1	$K_6C_5S_{11}N_5O_6$	"	"
1	$K_6C_6S_{12}N_8O_6$	"	"
1	$K_6C_7S_{12}N_8O_5$	"	"
1	$K_7C_7S_{14}N_7O_7$	"	"
1	$K_7C_7S_{14}N_{11}$	1890	*laevifolia.*

Even from the above incomplete summary it is sufficiently evident that the distribution of the frequencies of these anomalies would give half-Galton-curves. In

the first place, I have never seen fewer than four sepals or petals or divisions in the ovary, and never fewer than 8 stamens. The variation is solely on one side: at any rate it has been so during the nine years covered by the above mentioned observations, and since then as well. Trimerous flowers, which could hardly escape the attention of even the most superficial observer, are certainly not present.[1] The 'half Galton-curves' are obtained by considering variability of sepals, petals, etc. separately.

For the sepals:

21 K_5 4 K_6 2 K_7 Total, 27 flowers.

For the petals:

23 C_5 3 C_6 3 C_7 Total, 29 flowers.

For the partitions of the fruit:

18 O_5 3 O_6 1 O_7 Total, 22 fruits.

I have often seen pentamerous fruits, not only at Hilversum but in my own cultures. They were especially common in *O. Lamarckiana* and *O. laevifolia*; but I have seen them in the other species as well. I have rarely seen 6- and 7-partite fruits, and 8-partite ones never, so far.

The curve for the stamens in the above table turns out somewhat differently:

2 S_9 21 S_{10} 1 S_{11} 2 S_{12} 2 S_{14} Total, 28 flowers.

But we must bear in mind that the numbers of stamens are usually even. Now if we omit the odd numbers, as we did with the split petals, we get a beautiful half-Galton-curve: 21 S_{10} — 2 S_{12} — 2 S_{14}.

[1] In *O. biennis* I sometimes, though very rarely, found trimerous and even bimerous flowers. I have also seen some in my hybrid cultures. See also, A. Weisse, on *O. biennis* (K_3 C_3 S_6 G_3) in Verhandl. Brandenb. Jahrg. 39, 1897, p. XCIV with figure.

The stigmas behave in exactly the same way:

6 N_5 7 N_6 5 N_8 1 N_{11} Total, 19 flowers.

This curve would have to be reduced in the same manner. An increased number of stigmas (or of the divisions of the stigmas) is however so common in ordinary tetramerous flowers that the above cases are insignificant compared with them. Flowers with 5-8 stigmas are common; and as a rule all or most of the flowers on a single plant have these high numbers; but I very rarely found flowers with 9, 10 and 11 stigmas. The variation in the number of stigmas is therefore also describable by a half Galton-curve.

Fig. 109. *Oenothera Lamarckiana.* Pitcher formation on a fasciated plant, 1892. The pitcher is inserted close to the base of the lower leaf; but more than half of its stalk is fused to the main stem.

The tendency of the parts of the flower to polymery has therefore been latent in *Oenothera Lamarckiana* and in the various families during the whole period of my investigations.

Some Rarer Partial Deviations on Vegetative Parts.

Leaves with two apices and split median veins occurred in 1887 and 1888 on the field at Hilversum, in 1887 in a tricotylous *O. lata,* in 1892 in a tricotylous *O. laevifolia,* and repeatedly since in the various cultures.

Pitcher formation came under my notice ten times altogether, in 1887 and 1892 in the field at Hilversum, in 1889 and later in my own cultures. The first two pitchers occurred on fasciated stems (Fig. 109), the third on an *O. lata,* two on *O. laevifolia* (1891, 1895), two on *O. albida* (1898), two on *O. Lamarckiana* (1891, 1895), and one on *O. nanella* (1897). In these cases the pitcher usually took the place of a leaf about the middle of the stem when the plant was in flower, that is to say below the inflorescence; but the point of attachment to the stem always seemed to have been displaced upward. The pitchers were small, usually from 1 to 3 centimeters long; their dorsal side being usually three times as long as the ventral. They were set on long thin stalks about 3 centimeters in length.

Pitcher formation was also observed in the first leaves of young seedlings. Ascidia also occurred in *O. biennis,* in *O. Lamarckiana* × *biennis* (1896) and *O. Lamarckiana* × *suaveolens* (1897). In 1897 I found in a fairly small culture of *O. hirtella* five young plants with a pitcher on the top of the stem which interfered with the flowering of the main shoot.

This repeated, though rare, appearance of the phenomenon, scattered as it is pretty evenly over the various families, points to the conclusion that it is inherited in a latent state.[1]

Concrescence of two successive leaves on the stem also occurred, though rarely: I first saw it in 1887. Synanthy in the axils of leaves which had become concrescent or at any rate grown too close together, sometimes oc-

[1] *Over de erfelykheid van Synfisen,* Kruidkundig Jaarboek Dodonaea; T. VII, p. 129; for *Oenothera* see p. 165.

curred, forming structures which looked like fine double flowers.

A leaf was sometimes fused longitudinally with the stem, with the result that that part of the stem, to which the leaf was attached, was checked in its growth and bent in a most remarkable fashion. I observed a case of the concrescence of an axillary shoot with the main stem in 1899.

Fig. 110. *Oenothera rubrinervis.* A flower with two bracts; the lower one, the larger of the two, on the fruit pedicel, the upper on the fruit itself. The bract, in the axil of which the flower arose, is not shown.

Rarer partial variations in the flowers. A leafed and stalked fruit occurred in the tricotylous culture of the *O, rubrinervis*-family (Fig. 110). The stalk was 7 millimeters long and bore a leaf (*a*) whose median axis coincided with that of the bract in whose axil the flower arose. This leaf, which was situated on the side of the main bract was 7 cm. long and 1.5 cm. broad. The

second leaf was inserted about in the middle of the length of the capsule on the somewhat concave side of it, facing the main stem; it was quite small (*b*), being only 2 cm. long and 4 cm. broad. Bract and flower were otherwise quite normal.[1]

The existence of two flowers (and their fruits) in the axil of a single leaf is a very rare phenomenon. When it occurs, the upper, much larger, flower of the two is to be regarded as the normal one, whilst the lower, smaller one, which flowers much later must be supposed to arise as an accessory bud (Fig. 111). Whether this supernumerary flower is to be regarded as a shoot arising in the axil of a leaf which has remained undeveloped but corresponds in its position to the above described supernumerary leaf must remain for the present unsettled.[2]

Fig. 111. *Oenothera Lamarckiana.* Two fruits in the axil of a leaf. The lower, outer one is the youngest.

I observed this case of serial axillary buds not only on the field at Hilversum (1887) but also in my cultures, viz., in *O. Lamarckiana,* in *O. laevifolia* and in one or two other new species and crosses. In the latter they were particularly numerous in 1900.

The free tips of the sepals are sometimes broadened and take on the form and color of a leaf. I observed this in my cultures of 1889, 1894, and later. The sepals themselves may, on the one side, assume the character of a petal (1889). The petals themselves sometimes have outgrowths projecting from their median axes

[1] It is perhaps not superfluous to recall the fact that *Oenothera* has no prophylls (Eichler, *Blüthendiagramme,* II, 458) and that normal prophylls are inserted not medianly, but laterally.

[2] Russell, *Recherches sur les bourgeons multiples,* Annales des Sc. nat., 7 Serie, T. VII.

(1887). Cases are not rare in which supernumerary petals are formed by the transformation of one longitudinal half of a stamen into that of a petal. I found cases of this at Hilversum in 1886 and 1887, and afterwards in my cultures. Usually only one such organ is present in a flower but sometimes more, and once I observed as many as four (1894). There also occurred stamens which took on the form of petals by both the filament and the anther becoming flattened (1887, 1888 and later in the cultures). Cases of the fusion of two

Fig. 112. *Oenothera Lamarckiana.* Buds in the forks of split cotyledons.

Fig. 113. *Oenothera Lamarckiana.* Bud in the fork of a split cotyledon. The bud has grown up to a strong lateral rosette; its base has much swollen in consequence.

filaments together, and of the fusion of a filament with the pistil are fairly rare. I observed the former in 1887, the latter in 1894.

As the foregoing summary shows, the common floral malformations occur in *O. Lamarckiana.* I mention them briefly because I have not laid great stress on ob-

serving them minutely: if I had, this list would have been considerably longer.

The occurrence of buds on the cotyledons is the last example of one of these commonly recurring anomalies that I shall give. The young plants sometimes come up with three cotyledons (p. 474), sometimes with two, of which one is more or less deeply split. In the latter case a small bud is sometimes formed in the fork of the split, which looks most extraordinary, especially when the unsplit part of the cotyledon is fairly large. I first saw this phenomenon in 1897; since then I have seen about a dozen examples of it (Fig. 112). Sometimes I succeeded in growing these seedlings to maturity and in getting the adventitious buds to develop; they behaved like ordinary rosettes, and it was sometimes difficult to distinguish them from rosettes duplicated by fasciation (Fig. 108) without separating out the parts in question.

Our figure 113 shows a rosette of this kind in July, i. e., three months old (1900). The cotyledon was deeply split but single at the base. The base of the adventitious rosette and its connection with the cotyledons are much swollen; so that it seems to come very close to the main group of leaves, but as a matter of fact it is quite sharply separated from it.

This latent capacity to produce adventitious buds seems to be widely distributed in my cultures.

The facts recorded make it perfectly evident in my opinion that the potentialities for a series of anomalies are inherited in a latent condition in my *Oenotheras.*

§ 31. THE HYPOTHESIS OF A PREMUTATION PERIOD.

The mutations of *Oenothera Lamarckiana* which have been described in this section form so circumscribed a group of phenomena that the question as to their origin and causes can hardly be avoided.

There can be no doubt that I have neither witnessed the beginning nor the end of these mutations. I have evidently only been able to follow a section of the whole period of mutation.[1]

But in attempting to form some conception as to the mode of origin of such a period we must leave the sphere of observation for that of hypothesis. If the purpose of doing so was nothing more than the mere elaboration of the theoretical conceptions I should drop it at once. But, as a matter of fact, what we want is a working hypothesis which may result in bringing the origin of such a period within the range of experimental inquiry.

In order to work out some such hypothesis we must look to the facts to indicate what we must expect to find, that is what we really have to investigate.

We came to the conclusion in the preceding sections that a mutation is not the result of the sudden origin of a new character but of the manifestation of one already present in a latent condition. During the whole period of mutation the capacity for producing dwarfs is, apparently, present in all individuals. So is that for giving rise to examples of *lata*. On the other hand the capacity for producing *O. brevistylis* and *O. laevifolia* was, presumably, absent during the whole period of my experiments. Moreover a number of possible, or at

[1] Which is still lasting (1908).

least conceivable mutations did not appear—e. g., white flowers.

Our conclusion is therefore that only what is already present in a latent state can appear during the period of mutation; but nothing or almost nothing which is not already there.

Oenothera Lamarckiana would appear therefore to be laden with a certain number of latent characters, which it splits off if we may so express it, from time to time. Thus it may perhaps sometimes "split off" plants which lack one or more such latent potentialities, and therefore be no longer mutable in respect of these. If these individuals should be the only ones which ultimately survive, the mutation period would be at an end.

When and how did the latent characters arise? Their origin was the real beginning of the period of mutation, and will be referred to in future, for the sake of brevity, as *premutation.* This premutation or the first origin of the potentialities of the later mutations is evidently an event which takes place in a latent state. It may be accompanied by mutations; though that does not seem to be essential. It can of course only be made known to us by mutations; but it may be already there before we can perceive any trace of it.

We may assume that all potentialities which are manifested during a period of mutation arise either successively or at once. It seems possible that the whole group of new potentialities might arise in the lifetime of a single individual, or perhaps in the brief period of its sexual life. But it is also possible that several generations may be necessary for the process.

The older plant-breeders thought that it would be possible to upset the internal economy of a plant in such

a way as to make it highly variable or mutable. Louis Vilmorin, who used the French word *affoler* for this operation, proposed the following method:[1] Look through a crop for individuals which differ most from the normal in any direction, not necessarily the one leading to the ideal aimed at. Sow its seeds; and in the crop raised, do not, as in ordinary selection, choose the individuals which deviate most in the same direction, but such as are abnormal in the opposite one. Repeat this mode of selection through a series of generations and it is anticipated, says Vilmorin, that the variability will gradually increase, until finally it becomes so great that it will give rise to any new character desired.

It does not appear that Vilmorin carried out such an experiment and still less that he ever saw the result he anticipated.

Nevertheless his suggestion deserves attention; it may contain the germ of truth. And anyhow the method would be likely to lead to the discovery of latent mutations.

One of the most important conclusions which may be drawn from these general considerations is that a premutation must be due partly to internal and partly to external causes. The former determine what shall arise; the latter when it arises.

The external causes must be other than the ordinary conditions of life under which the species remain constant. On the other hand they must be such as appear not too rarely in the natural state. I assume these causes to be perhaps a combination of extremely favorable with extremely unfavorable influences: this view would at any

[1] Louis Vilmorin, *Notice sur l'amélioration des plantes par le semis.* Nouv. Edition, 1886, p. 36.

rate account for the comparative rarity of their appearance.

We should therefore have to determine, experimentally, the effect of the combination of such extremes. I do not regard this as in any way impossible. For example, take very weak buds and their shoots, or very weak flowers and supply them with as much nutriment as possible. Just as saplings or the strong shoots produced by resting buds, often develop hitherto latent characters (such, e. g., as the well-known intermediate forms between leaves and thorns in the common barberry); so perhaps they might also be induced to give rise to mutations. A very rapid multiplication is generally regarded as an effective inducement to the production of mutations; the reason for this being probably that the seeds which would otherwise perish at or immediately after germination find the necessary conditions for full growth. The seeds in question are those which have suffered from unfavorable circumstances; and this gives us the contrast we spoke of above. For the sake of experiment, therefore, we should collect the seed from the small, late, lateral twigs of the higher orders, and sow it with all possible care.[1]

Let us now suppose that a genuine premutation period has been induced or at any rate discovered. What must be expected? In other words let us suppose that the potentialities for a whole series of mutations have arisen in a plant or a group of plants. Will each potentiality actually give rise to a mutation, and, hence, to a new species (fit or unfit)? Chance will obviously have a great deal to do with it. The latent characters are evidently

[1] Experiments of this kind would obviously have to be continued through some years; the greatest difficulty is the choice of suitable plants.

not affected by the struggle for existence in which the organisms bearing them are engaged; they do not weigh in the scale on the one side or on the other. They multiply or perish precisely as their bearers do. But one *Oenothera*-fruit may bear between one and two hundred seeds; and a vigorous plant bears hundreds of fruits. So that it practically never happens that all the seeds produced become flowering plants. It is very largely a matter of chance which of these survive, and therefore a matter of chance which latent mutations continue and which perish.

I conclude from this that the number of mutations actually observed is no measure at all of the number which presumably arose during the premutational period.

We must think of the origin of groups of closely related species in other genera and families as essentially analogous to the mutational period in *Oenothera Lamarckiana*. Examples of such groups are the long series of elementary species, our knowledge of which we owe to JORDAN and his pupils; and the well-known nebulous groups of the old systematists such as FRIES, NÄGELI and others. It is reasonable to suppose that the numerous elementary species of *Draba verna* all arose in a single period in a small locality and that they have spread thence, hither and thither over the whole of Europe.[1] Or perhaps they have arisen during the period of distribution. The same may be said of *Viola tricolor*, *Helianthemum vulgare*, etc. The whole appearance of *Draba verna*, at present,points to a period of mutation of exactly the same kind as that of *Oenothera Lamarckiana*.

[1] A few species of *Draba verna* ought to be cultivated side by side in every botanical garden. Their differences and constancy are perfectly obvious and such as to strike the eye of every visitor. I have only two species in cultivation; but even those have been of general interest already.

The genera *Rosa, Rubus, Hieracium, Salix* and some other types rich in species formed the nebulous groups of the older systematists: they were extremely rich in forms that could hardly be distinguished. Without cultivation we can only have a provisional knowledge of their species and the cultivation of some of these forms through even a few generations would be no light task. But the richness of forms (exclusive of hybrids), is comparable to that of *Draba verna* and *Oenothera Lamarckiana,* and clearly points to the existence of mutation periods, belonging partly to the past and partly perhaps to the present.

The most conclusive point of all is however the necessity of assuming such a period to have occurred in the group of *Oenothera biennis* (the subgenus *Onagra*), which is absolutely analogous to the *Lamarckiana*-group (see p. 440).

Finally, a few words must be devoted to the question as to when the premutation period occurred in our particular case of the *Oenothera Lamarckiana* at Hilversum. Two possibilities present themselves. Either the plant was already in a period of mutation when its seeds were first sown there by Mr. Six (in about 1870, see p. 266). Or the period began on the spot. In the former case the *Oenothera* must have already been mutable and this property had simply escaped observation. This seems hardly likely because *O. nanella, O. gigas* and *O. laevifolia,* if they had come under the eyes of nurserymen or amateurs, would certainly have been thought worth cultivation, and would have been put on the market. But no "varieties" of *O. Lamarckiana* occur either in descriptive works, or in catalogues.

In the latter case; we should suppose that the rapid

multiplication of our *Oenotheras* between the years 1870 and 1886 (p. 266) was the cause of the appearance of the premutation period and therefore the beginning of mutability in this case. And this supposition agrees so well with the little that we know about the origin of species in general that it deserves attention, to say at least, until definitely disproved.[1]

We may sum up the foregoing in the generalization that each mutational period is initiated by a premutational one, in which the new characters, which are to appear, arise in a latent condition under the influence of external causes.

[1] Afterwards I found that seeds of *Oenothera Lamarckiana* from other sources, especially from the strains of different nurseries, may produce the same mutations. From this I conclude that the period of mutation must be older than the occurrence in the field at Hilversum, and probably as old as the introduction of the present strains into European gardens, which was effected by Messrs. Carter & Sons about 1860 from seed, gathered in Texas. (See *Berichte der deutschen Bot. Gesellschaft,* 1905, Bd. XXIII, p. 382.—Note of 1908.)

V. CONCLUSION.

Perhaps the most important general result of my observations on the origin of species in the genus *Oenothera* is the proof which they afford that this phenomenon can be dealt with experimentally. Hitherto the general opinion has been that this extraordinarily important phenomenon was amenable neither to direct investigation nor even to direct observation. The experience of horticulture is sufficient to demonstrate the fact that new forms do sometimes appear and less rarely perhaps, than is imagined. But when they appear it is too late to attempt to discover how they arose. We may try to explain how this happened, but it is no longer possible to deal with the question experimentally.

For this object it is necessary to have a plant which happens to be in a mutation period, i. e., which has the power of giving rise repeatedly to new species. Such plants had hitherto not been found.

The way to look for mutable plants is to make very extensive sowings of various species. Seeds are collected either from wild plants or from plants that have run wild or lastly from cultivated plants which one has oneself grown for a sufficient length of time to make certain that they are free from the effect of any previous crossings that may have taken place. I have either collected the seeds in the field, or transplanted a few plants into

the garden and allowed them to bear fruit in a state of perfect isolation. We can be guided, to a certain extent, in our choice of species by observations in the field; either by finding new varieties or subspecies; or by a certain richness in partial variations, or by so-called monstrosities. The latter are due to latent potentialities which are manifested from time to time on isolated twigs, leaves, etc. It is natural to conclude that where such latent potentialities occur in unusually large numbers, others may be expected and, amongst them, those that we are looking for.

I have conducted a considerable number of such experiments, both before and after I began my main experiment, particularly with species of our indigenous flora, on such a scale as the amount of seed harvested would allow. For example, I sowed seeds of *Capsella Bursa Pastoris, Sisymbrium Alliaria, Daucus Carota, Cynoglossum officinale, Verbascum thapsiforme, Aster Tripolium, Bidens cernua, Thrincia hirta, Crepis biennis, Centaurea nigra* and a whole series of other wild species. They were mostly forms which attracted my attention by the possession of fasciations, concrescences, or other kinds of abnormality. I cultivated the monstrosities for longer or shorter periods of years in order to test their hereditary nature.

Almost all the species proved themselves to be immutable.[1] I conclude from this that most of the wild species in our neighborhood happen to be in an immutable state. In other places the same species may of course be mutable,[2] for, according to the theory, mutability is

[1] See also the first part of the second volume.

[2] This seems to be true of *Capsella Bursa Pastoris,* near Landau; see Solms Laubach, *Bot. Zeitung,* 1900, October part.

not an intrinsic character of a particular species, but a passing phase in which the plants in a particular locality may happen to be.

Only one species answered my purposes: *Oenothera Lamarckiana*. Even on the spot where I found it, it gave promise of a more favorable result than all the rest. In the first place, it was not a genuine wild form, but an escaped one, which had spread from a bed to a deserted field close by, where it had multiplied abundantly. A rapid multiplication of this kind is one of the supposed causes of mutability. In the second place it was very rich in partial abnormalities; not only in the common ones like floral anomalies, pitcher formations, fasciations, connations, adnations, etc., but in the rarer ones, like the development of secondary axil buds in the inflorescence and so on. In the third place I found isolated delicate plants with narrow leaves which only formed rosettes and then died. I was unable to study them further at the time but they have since turned out to be a perfectly good new species (*O. elliptica*). And lastly I found there two well characterized forms which were hitherto unknown and have since proved to be constant (*O. laevifolia* and *O. brevistylis*).

But the result of sowing the seed collected in the field, was decisive. I did this first in 1887 and repeatedly afterwards, but particularly in 1889. My very first culture gave me what I wanted; it contained a form, which differed sharply from the normal in almost every feature, which had not been seen in the field before and was otherwise also absolutely unknown. This was the *Oenothera lata*. In the following year I sowed the seeds of plants which I had brought with me from Hilversum in the autumn of 1886 as rosettes: they gave me the same form

O. lata and another besides, *O. nanella*; both were represented by several examples (p. 224). I sowed seeds, collected in the field, again in 1889 on a larger scale and again got the same two forms, and yet a third form, hitherto unknown, *O. rubrinervis* (p. 304). Later on I found the two former (*O. lata* and *O. nanella*) in the field as well (1894).

This rapid succession of discoveries decided me to practically give up the experimental sowings of the other species and to investigate *Oenothera Lamarckiana* as minutely as possible. Two methods of investigation presented themselves. On the one hand, observation in the field, together with a yearly sowing of seeds collected there. On the other, the cultivation in the garden of families of plants through many generations. I adopted the latter without however neglecting the former. And in this connection I wish to particularly emphasize the point that my cultures are nothing more than a repetition of what occurs in nature. My idea was merely to follow the natural process of the origin of new species as accurately as I could, by excluding, wherever necessary, the sources of error and uncertainty which are the unavoidable result of free fertilization by insects.

I have made observations in the field every year since 1886; I thus witnessed the origin of new forms, the majority of which, however, perished. They were essentially the same as those in my cultures. There is no reason for supposing that any forms arose, in my garden, which would not also have arisen in nature under sufficiently favorable circumstances. In nature there is not room enough for all seeds to germinate, still less to give rise to adult plants: so that the rarer and weaker sorts perish; whereas in my garden they are transplanted and

carefully tended. It is this fact, together with the exclusion of the visits of insects, which are the main advantages of the method of cultivation.

The experiment does not create anything new. It merely enables us to see and study what happens in nature.

* * *

A glance at my cultures shows the mutation period which I have studied to be a definite whole. It comprises a sharply circumscribed group of phenomena, narrowly delimited in every respect. I mean, the same events repeat themselves regularly; new ones occur but seldom, and when they do, they conform to rules already ascertained. We do not see a hopeless chaos of forms which merge into one another; nor is the variability an unlimited one. On the contrary we see a relatively small number of perfectly distinct and constant forms which we find appearing again and again.

There can be little question that I have witnessed neither the beginning nor the end of the period. Everything points to the conclusion that it was in full swing in the locality when I first visited it, and that the potentiality for everything which appeared later was already present there at that time. I did not see the majority of the forms during the first few years probably only because I was not on the look-out for them. For when once I had got to know a form I found it every year afterwards, with very few exceptions.

It is highly improbable that I have exhausted the whole wealth of latent potentialities in *Oenothera*. On the contrary it is possible that even the most beautiful and important mutations and those deviating most from

the type have, so far, escaped me altogether. I have hitherto only experimented with ordinary sowings; and my object has been rather to become familiar with the principles of mutation, than to bring to light a multitude of novelties.

I gradually came to see that the method of searching for mutations was capable of improvement in many respects. There seem to be two main ways of doing this: the choice of seeds and hybridization. If the harvest turns out to be meagre for one reason or another, or the fertility of the seeds diminishes greatly (that is to say only a small percentage remain fertile) the prospect of getting mutations in general, or at any rate of getting particular forms, seems to be considerably increased. For example in a sample of seeds which had been kept for 5½ years the fertility went down from 70 to 5 seeds per cubic centimeter; but the percentage of mutations went up from 1-5% to 40% (p. 263). In another culture only about 30 seeds germinated out of the whole harvest sown; but of these, 12 gave rise to mutants which formed therefore 40% of the population. And the view that crossing increases variability is generally held and seems to be supported by some of my experiments.

My cultures were conducted on the following lines. From seeds or plants which I gathered at Hilversum I derived my so-called families as follows: Seeds were collected every year from a few (e. g., 4-10) individuals. These were chosen as being typical examples of the families in question and were either left to be fertilized by insects on some isolated spot (1887-1894), or (as in later years) were protected from the visits of insects by parchment bags and artificially fertilized with their own pollen. It was only in *lata*-families that crossing always

took place (this species being exclusively female), the pollen of *O. Lamarckiana* being generally used for the purpose.

Thus each family has a single and pure main stock. Branches of it are to be regarded as separate families. The mutations arose from these main stocks.

The great advantage of this method is that it enables us to know the ancestors of each mutation through one or more generations. And this is just what is lacking in observations made in the field, and in horticultural data. The number of generations known is great in direct proportion as the date of the mutation in question is recent. The pedigree of every single mutation can be determined in my records, and found to be, for example, a pure line of *Lamarckiana,* or *laevifolia* or *rubrinervis* or *lata,* and so forth, according to the family.[1] One would like to complete the series of ancestors for the period of time previous to the year 1886, in which I first collected seeds and plants. I have no direct observations which will help us; but it is known that the plant began to spread over the field about 1870. It is highly probable that new forms, if they had flowered during these years, would have been found flowering afterwards in the field also, after the rapid multiplication which had taken place. We may therefore consider ourselves justified in mentally carrying back the pure unbroken line to 1870.

The individual mutations in the various families arise wholly independently of one another; that is to say each one arises directly from the main stem. If we harvest the seed of mutants, or fertilize other plants with their

[1] The pedigrees for the 3 chief families can be found on the following pages: *Lamarckiana*-family, pp. 224 and 262; *laevifolia*-family, p. 273; *lata*-family, pp. 285 and 288.

pollen, new lateral branches arise from the family; the members of such lateral branches are not henceforth called mutants. The independence is, however, only external, the analogous mutants being related to one another as sisters, or as nieces and aunts, etc. The identity of their features is obviously due to the fact that they originate from the same latent potentialities in the main stem.

But each mutation arises suddenly and directly from the main stem without any preparation and with all its characters.[1] Every new dwarf that appears is as small as the dwarfs of the fourth and fifth and later generations. Each *lata*-mutant is as purely female as the *lata* of the present day which has been cultivated for ten generations. The various *rubrinervis*-plants which I have cultivated during the course of many years for various purposes are indistinguishable from the newly arisen mutants of these forms. *O. gigas* only arose three times, *O. scintillans* fourteen times. But each time they appeared with exactly the same characters.

The occurrence of transitional and intermediate forms is a very important point. These do certainly occur; but they are phenomena of individual variability and not of mutability. For, in the first place, these transitions do not appear *before* the new species, but, at most, simultaneously with it; usually, however, not till well after it has arisen. These transitions are not therefore the steps which must be traced by a new form in its origination; this origin, far from being reached by these steps, is absolutely independent of them. The intermediate forms

[1] These characters are therefore to be regarded for each mutation as expressions of one single internal change. See § 13. pp. 327-330. For the relative frequency of the appearance of the various mutations, the so-called mutation-coefficients, see § 14, p. 337.

are not in fact what they are called, in the strict sense of the term; they are only more or less incomplete copies of a type already existing. They may be observed just as well in the later as in the earlier generations: in fact better, because there is little prospect of finding them at first, the number of mutants being so small. It is only when the latter can be propagated by an unlimited quantity of seed that complete series of transitional forms may be expected.

These transitions are partly atavistic phenomena, partly instances of ordinary variability; and partly of transgressive variability. An instance of atavism is afforded by *O. nanella* which may be characterized for the whole of its life by unstalked leaves, but which during a brief period of its youth exhibits the stalked leaves of its ancestors (see Fig. 78 on p. 362). This case is perfectly analogous to the well-known embryonic forms of many other plants. Atavism is, so to speak, accidentally brought about in *O. laevifolia* whose leaves, normally smooth, are sometimes crumpled, either singly or over the whole plant when it is an unhealthy one. Most characters exhibit transgressive variability more or less; but there is always a wide gap between the largest *O. nanella* and the smallest flowering *O. Lamarckiana.* The leaves of *O. gigas* exhibit a high degree of transgressive variability; they may be broader and narrower than those of the parent species and sometimes, even, come to resemble those of *rubrinervis* and other narrow leaved forms. Further, the size of the flowers varies directly with the vigor of the plants, in all the species.

If we deal with one character at a time we can make perfectly continuous series embracing *O. Lamarckiana* and all the species which have arisen from it. For ex-

ample for the breadth of the leaves, the length of the fruits, the size of the flowers, etc. But exactly the same can be done for those forms which have been recognized as species by the best systematists and exhibit such excellent points of difference as, for example, the size of the flowers in *Oenothera biennis L.* and *O. muricata L.*

The boundaries between my new species are no more obliterated by transgressive variability than are those between recognized types. The phenomenon is a very general one in the whole animal and vegetable kingdom; and is very apt to land any one who confines his attention to one character at a time, into difficulties. In settling the identity of a doubtful case situated in the borderland between two types the other characters of the doubtful individual must receive attention; for, in spite of the phenomenon of correlation, the other characters will almost always show to which side the doubtful form really belongs. And if this comparison does not suffice, we must resort to experimental sowings; the direction in which the offspring regress will leave no doubt as to the specific type to which the doubtful individual belonged.

In this respect as in all others, my new forms of *Oenothera* are species and not varieties; with the single exception of *O. nanella* (see § 18, pp. 360-363).[1] The difference between a species and a variety is that whilst a variety is marked by the possession of a single distinctive character a species or subspecies differs from its nearest allies in almost all its parts. Lack of pigment, hairs or spines; branching of leaves or stems; or an abnormal development of these characters; laciniate leaves and petals, etc.—such are the characters of true varieties. There are two further points about varieties. First the

[1] On this point see, especially, the second volume.

whole "habit" of the plant, in so far as it is not directly modified by the varietal character, remains unaltered; color varieties can only be recognized by their color; thornless ones only by the absence of thorns; and so forth. True species are on the other hand distinguishable from one another in almost every organ and at almost any age. Secondly, the character of a variety usually does not exhibit transgressions. White flowered varieties, although they often have a bluish or reddish blush in their petals, are almost always paler than the palest variants of their parent species. The very reverse is the case with specific characters of which the extreme variants may not only meet but often overlap.

New species differ from varieties in yet another way. The latter usually occur in several genera and families under exactly similar forms, which are as a rule, given the same or synonymous names. But I have sought in vain for forms analogous to my new species with the single exception of the dwarfs. Perhaps also, *O. laevifolia* which is distinguished by the absence of crumples in its leaves, and *O. brevistylis* with its partial loss of the inferior ovary should be regarded as true varieties; they are just the two forms which have never arisen in my cultures. But apart from these, the new species are without parallel either in the genus *Oenothera* or elsewhere in the vegetable kingdom.

If we regard varieties as having arisen by the loss (or latency) of an old character, it seems reasonable to regard species as having arisen by the origin of a new one.

The question as to the constancy of the new forms is one of the greatest importance. And it may be stated straight away that the character is not one which is attained by repeated selection. The view that at least a

great many subspecies and varieties are not, or at any rate not yet, constant and that they revert to the parent species from time to time is commonly held. It is this that is meant by the statement that varieties are incipient species. This conception is however entirely erroneous.

My new species are either absolutely constant from the beginning, without the slightest trace of reversion; or, when they are not, exhibit no increase in constancy, in response to selection.

In order to test the constancy of the new forms directly after their arising from *O. Lamarckiana* or other families one has to artificially fertilize the mutants themselves with their own pollen. Large quantities of the seed are then sown; and as the new species is easily and certainly recognized during the first months of its life, before it develops a stem, some hundreds or even thousands of seedlings can be recorded. Of these only as many as can be conveniently accomodated are chosen, at random; and cultivated until they flower and ripen their fruits. The constancy of a new form can be determined by growing it in this way for a number of generations. From the very beginning *O. gigas, O. rubrinervis, O. oblonga, O. albida, O. leptocarpa, O. semilata* and *O. nanella* were absolutely constant.

O. scintillans, O. elliptica and *O. sublinearis,* on the other hand, proved to be inconstant. Only a small proportion of the seeds of these forms repeat the parental type. The others revert to *O. Lamarckiana* or produce other mutations. *O. scintillans* usually did not repeat itself in more than 30% of its offspring and could not be got to increase the proportion by continued selection; the others did not furnish sufficient seeds for conclusive experiments.

Inconstant species[1] do not seem to occur in nature. And if they did, they would be bound to disappear sooner or later because the atavists, which they produce every year, would probably be constant, and soon supplant the inconstant form.

We see therefore that in the process of the origin of new species some certainly do arise which are not capable of existence for any length of time. Nature does not confine herself to producing just what is wanted; her creative power seems to be almost unlimited. She furnishes every possibility, so to speak, and leaves it to the environment to choose what suits it. In other words mutability is indiscriminate.

Could the new species maintain themselves in nature? This is a question which naturally presents itself. I have conducted no experiments in this direction. But it is a fact that *O. laevifolia* and *O. brevistylis* have survived the struggle for existence at Hilversum for a long period of time.[2] In my garden the plants certainly appear to be less resistent than they would be in nature, partly on account of the amount of manure they get, partly because there is no selection which kills off the delicate ones in early youth, and partly and in fact chiefly, on account of my preference for annuals. For example annual *oblonga* set far too little seed; biennial ones give a good harvest. *O. rubrinervis* as an annual is very brittle, as a biennial very strong; and so forth. Both these and *O. gigas* would maintain themselves well in nature if they grew in the biennial form; and would perhaps form just as good species as the forms imported from America, *O.*

[1] For the justification for this expression see § 19, pp. 377-379.

[2] They are still seen to be growing in the field at Hilversum. (Note of 1908.)

biennis and *O. muricata*. *O. albida* would certainly be too weak; and the inconstant and sterile or partly sterile forms would obviously perish sooner or later.

But direct investigation is necessary before a satisfactory answer to this question can be given.

Lastly, let us examine my results from a theoretical standpoint. Two points stand out prominently. First, the question as to the origin of the whole mutation period; and secondly the analogy between the phenomena observed and the origin of species in general.

We regard the beginning of the mutation period as the time when the latent potentialities, present in this period, first arose. For obviously the capacity for producing *O. gigas* has not been a property of all the ancestors of my *Lamarckiana*; it must have arisen at some time: and similarly with the other species. Are these potentialities as old, or perhaps even older than *Lamarckiana* itself? Probably not. It is simpler to suppose that they either arose on the spot where they first appeared, or a little earlier in the life of the species.

I call the origin of the latent potentialities, Premutation; the mutations themselves are only the expressions of these. One of the objects of future investigation ought to be to determine the essential conditions of this premutation and if possible to induce it at will.

Periods of mutation must occur, or at any rate must have occurred, times without number, in nature. For groups of allied species, which, so far as one can judge, are related to one another exactly as my *Oenotheras* are, occur throughout the animal and vegetable kingdom. Wherever the constancy of the characters of such species has been established in cultures they constitute the *espèces affines* of JORDAN. I have, already, often men-

tioned *Draba verna, Viola tricolor, Helianthemum vulgare,* etc. as the best examples of these. But in cases where the constancy of the new species has not been experimentally tested, or where their study has been made difficult by the effects of natural crossing, we get the so-called nebulous groups of the systematists — i. e., groups in which the various authorities do not agree with each others' diagnoses. *Salix, Rubus, Rosa, Hieracium* are the most familiar examples of this case.

But the most important point for us is the almost complete agreement between the new *Lamarckiana*-group and the old *biennis*-group. The forms of the latter, regarded by some authors as species and by others as varieties, give the impression of being the remains of a previous mutation period. They obviously belong together, differ from one another in the same kind of way as the newer species do; they are constant, mutually fertile, and exhibit transgressive variability in many of their characters in such a way that at first sight they do not seem to be sharply separated from one another. Nevertheless they come absolutely true from seed.

The supposed mutation period of *Oenothera biennis* must obviously have taken place in their American home; the products of this period, the Linnean species of to-day, have spread, thence, over a large part of the earth.

And if we give the rein to our imagination we can conceive each genus and each larger group as being, also, the result of a mutation period.

PART III.

NUTRITION AND SELECTION.

I. SIMULTANEOUS INFLUENCE OF NUTRITION AND SELECTION ON VARIOUS CHARACTERS.

§ 1. VARIABILITY AS A NUTRITIONAL PHENOMENON.

When a new science comes into the field, it usually happens that certain groups of phenomena, which up to then had been dealt with under other heads, are found to come within its ken. This is happening at the present moment, with the study of variability and that of the dependence of the growth and development of particular organs and characters on nutrition. This connection with nutrition has been studied chiefly from the experimental and biological point of view; whilst the same phenomena have been dealt with by statistical methods from another point of view.

New boundaries are difficult to define, and it will be a long time before an agreement will be reached as to which sections of the theory of nutrition should be included in the science of variability.

In the historical and critical part (Part I, pp. 133 and 137 etc.) I have urged that we had no right to give up the attempt to provide an answer to the question as to the causes of the fluctuating differences between individuals and between homologous organs of one and the same individual. The science of variability must not be satis-

fied with being a purely descriptive and statistical one; it must, like every other, seek to determine the causes of the phenomena of which it treats.

If polymorphism is excluded on the one side and mutability on the other, the whole range of variability can be described in terms of QUETELET'S law. Then there is the question of the inheritance of these variations. The deviations of the various individuals from the mean are heritable: but not in their entirety; a part is always lost. Regression always takes place, and this usually involves more than one-half and often as much as two-thirds of the original deviation. This is the source of the third principle in the theory of variability: the possibility of an increase of the deviation by means of selection. This increase, which is sometimes spoken of as a heaping up of similar small differences, leads to the so-called accumulation and fixation of characters and thus to the production of improved races.

Exactly the same deviations from the mean as those with which statistics have made us familiar may be brought about, either by chance or by deliberate experiment, by changes in the conditions of nutriment. Characters and organs whose dimensions may be increased or diminished by selections, are also dependent on the conditions of life and in many cases it is very difficult to decide which of the two causes has been most operative.

The recent researches of MAC LEOD and others clearly point to a very close relationship between nutrition and variability. For, broadly speaking, variability is really nothing more than differences in individual strength. The stronger a plant or a branch on a plant is, the greater is the likelihood of deviations in a positive direction; weak

plants and sickly branches tend to fluctuate in the opposite direction.

But "individual strength" points clearly to nutrition, if we use this word in its widest sense and especially if we make it include the better opportunity which a plant has of being nourished, as when it has plenty of room and plenty of light, and so forth.

If we view the whole field of nutritional phenomena and that of fluctuating variability[1] they appear to interlock only to a certain extent. Many statistical inquiries point as little in the direction of such a connection, as the excessively vigorous or feeble growth of weeds and cultivated plants under extreme conditions seem to point to it. But indications that the two phenomena are in fact connected, are by no means lacking. GOEBEL, for example, observed that in *Agrimonia Eupatorium* the lower, best nourished, flowers of the inflorescence had many more stamens than the upper more feebly nourished ones.[2] In the sugar-beet the capsules on the lower part of the stem contain many seeds; those on the upper part and on the small lateral branches contain few, and often only one. Many varietal characters answer the requirements of the gardener only when they are on strong individuals; if the plants are weak they are developed either too little or not at all (e. g. *Celosia cristata*).

We must make it our business therefore, on the one hand, to study the results of increased and diminished nutrition, by statistical methods; and on the other to deal with the conditions affecting the different groups of individuals, when studying QUETELET's curves.

An inquiry of this kind will at any rate have one

[1] See C. FRUWIRTH, *Die Züchtung der landwirthschaftlichen Culturpflanzen*, 1901.

[2] GOEBEL, *Bot. Zeitung*, 1882, p. 357.

good result: it will bring out more prominently the fundamental distinction between variability and mutability. There are still so many cases in which it is difficult or even, for the present, impossible to define the limits between these fundamentally different principles, that every contribution to a solution of the problem is of value.

Therefore it is most essential from the point of view of the theory of mutability to have a perfectly clear conception of the nature of variability in the narrower sense of the term. Absolute constancy and high variability are regarded by many as diametric opposites; in fact it is believed by those who hold the modern theory of selection, that variability leads to inconstancy, that is to say to the production of new forms. According to the mutation theory however constancy and variability are perfectly compatible and, in most cases, usually associated. That which is constant is the type or mean, on both sides of which fluctuations may occur.

The ray florets of the common cornflower are variable in number; the weaker the plant or branch the smaller is this number, according to Mac Leod.[1] The secondary fruits of *Papaver somniferum polycephalum* exhibit the same correlation,[2] the tongue-florets in the heads of *Othonna crassifolia* diminish if the nutrition of the plant is artificially curtailed.[3] The same thing happens in *Chrysanthemum segetum*[4] and other Composites.[5] And

[1] Page 135 of this book. [2] Pages 138-143.

[3] Page 147 and *Othonna crassifolia* in Kruidkundig Jaarboek, Gent, 1900, p. 20.

[4] *Over het periodisch optreden van anomalien,* Kruidkundig Jaarboek Dodonaea, T. XI, 1899, p. 54; *Sur la périodicité des anomalies dans les plantes monstrueuses,* Archiv. Néerland. d. Sc. exactes et nat., 2d Series, T. 3, p. 403. *Ueber Curvenselection bei Chrysanthemum segetum,* Berichte d. d. bot. Ges., Bd. XVII, 1899, p. 84; *Ueber die Periodicität der partiellen Variationen; ibid.,* Bd. XVII, p. 45.

[5] A. Weisse, *Die Zahl der Randblüthen am Compositenköpfchen,*

we can easily observe that in the Umbelliferae the number of umbels is small in proportion as the twig, bearing them is weak.

With regard to *Papaver somniferum polycephalum* we saw in the first part that it was not possible to separate selection from nutrition. I mean, if we choose our seed-parent, paying attention to the greater or less beautiful development of the circlet of secondary fruits, we inevitably chose either the strongest or the weakest plants. There seems therefore no escape from the conclusion that the variability of this circlet is simply a phenomenon of nutrition and that selection in one direction merely chooses the most highly nourished individuals; and in the other, the most poorly nourished.

In an investigation of this kind one must take into account the susceptible period. One organ will pass through this period earlier; another later, as I have pointed out in the case of the poppy referred to. The same is true of oats and wheat in relation to the amount of water in the soil. In the first vegetation-period this condition influences the number of internodes in the haulm as well as in the panicles, or ears. At the time of shooting, the amount of water in the ground affects the length of the internodes, and the size of the parts of the inflorescence (the foundations of which have already been laid down by this time) as well as the greater or less fertility of the ears. Much water at the time of shooting increases the amount of straw as well as the yield in grain.[1]

Jahrb. f. w. Bot., Bd. 30, 1897, p. 453 and W. Haacke, *Entwickelungsmechanische Untersuchungen,* Biol. Centralbl., 1900.

[1] Von Seelhorst, *Journal für Landwirthschaft,* Bd. 48, p. 163; Reference in *Botan. Centralbl.,* 1900, No. 41, Bd. 84, p. 54.

The truth of the theory put forward by SCHINDLER and VON PROSKOWETZ that it is impossible to unite many good qualities in one individual, depends partly on the absolute productive capacity and partly on the correct nourishment of the individual qualities at the sensitive period of their development. JOHANNSEN's exhaustive and epochmaking researches into the correlation between seed-weight and nitrogenous contents of barley point in the same direction. The heavier the grain the greater is the amount of nitrogen which depreciates the value of the grain.[1] Evidently both vary in the same direction under the influence of high nutrition. But if the sensitive periods for the two should not coincide, the supply of nutriment might be so managed that the weight of the seed is increased without effecting a corresponding increase in those constituents of the seed which are rich in nitrogen. At present it is not possible to do this directly, but JOHANNSEN succeeded in getting a much better harvest without having increased its proportion of nitrogen, by selecting the one value in a positive direction and the other in a negative one.

A further series of experiments is necessary before the conclusions (important alike to the pure and applied biologist) based on these remarkable results can be regarded as thoroughly established. I am simply using them here as a proof of the relation between nutrition and selection in general.

For there is yet another method of studying the relation between manuring and selection. We can alter both factors; and allow them to operate either in the

[1] W. JOHANNSEN, *Ueber die Variabilität der Gerste mit besonderer Rücksicht auf das Verhältniss zwischen Körnergewicht und Stickstoffprocent.* Meddelelser fra Carlsberg Laboratoriet, Bd. 4, Heft 4, 1899.

same or in opposite directions. We can, so to speak, add their effects or subtract the one from the other. If this experiment succeeds it proves that the two phenomena are of the same order, and suggests a method of determining their relative importance.

I shall therefore describe in this chapter a series of experiments carried out on this principle. They deal with measurable or countable characters which are capable of experimental as well as of statistical treatment. I chose for this purpose the length of the fruits of the ordinary *Oenothera Lamarckiana* (Figs. 114 and 115, pp. 529 and 530), and also the material employed by Ludwig which is afforded by the ray florets of Composites and the rays in the umbels of Umbelliferae (Figs. 117-119, pp. 561-565). In the case of the fruits I tried both the addition and subtraction of the factors; but in that of the ray-florets and the rays of the umbels only the simultaneous operation in opposite directions of heavy manuring and negative selection. The result of the experiment was that sometimes the one factor and, at other times, the other predominated.

The inquiry into the effect of nutrition (manuring, plenty of room, light and water, etc.) has led to the discovery of two principles (foreshadowed in the discussions in the first section p. 137) which I think ought to be enunciated here in the interest of a clear understanding of the whole range of phenomena.

These two principles are the following:

1. The younger a plant is the greater is the influence of external conditions on its variability, that is, on the place which its various characters will occupy in the curves of variability of the whole culture or race.

2. In connection with this principle the nutrition of the

seed on the motherplant has, in many cases at any rate,[1] a greater effect on variability than nutrition during germination and vegetative life itself.

It seems to me that these principles which I only appreciated after many years of experimenting, are now perfectly clear and evident.

From these principles there follows the experimental method which I call the *Principle of the manuring of the parent-plant.* That is to say, the effect of manuring on variability must be studied not only on the plants which have been heavily manured, but mainly on the generation produced by their seeds.

These principles lead to a further problem, the solution of which will perhaps be of great importance from the point of view of the theory of selection. For it is clear that the principle of the manuring of the parent-plants is not necessarily confined to one generation. We shall obviously not get the best nourished seeds from ill favored parents; that is from parents which have themselves arisen from poor seeds. On the contrary the operation of high nutrition of the seeds must be capable of accumulation through two or more generations. The same is true of low or defective nutrition. But inasmuch (as a general rule) those individuals which exhibit the character dealt with in a high degree are the best nourished we naturally choose the most highly nourished individuals as seed-parents when we are selecting for any particular character. In the course of generations the effect of nutrition accumulates, and in this way the deviation of the particular character from the original type is continuously increased. The question arises therefore:

[1] Sometimes, however, a greater effect can be produced on variation by a good or bad treatment of the seedlings than by the choice of seeds; for example in *Papaver somniferum polycephalum.*

what part of the result of selection is due to this accumulation of nutrition during the succeeding generations?

These considerations tend to draw selection and nutrition closer and closer together. The exact mode of nutrition seems to me a matter of secondary importance; what is of the first importance is to discover the effects of nutrition on the susceptible periods in development, and to study the accumulation of this effect in the course of some generations. Now, just as nutrition reaches its maximum effect, in practice, in the course of a few generations, so the limit reachable by selection is very soon attained.[1] The significance of the parallel between these two limits seems to me to be obvious.

The closer variability is drawn towards nutrition the wider becomes the gulf between variability and mutability.

§ 2. METHODS OF INVESTIGATION.

The effect of nutrition and selection can either be exerted in similar or in opposite directions; the sum of, or the difference between, their effects can thus be determined.

The general effect of both factors is well known. We are not concerned to prove that the effect of high nutrition is to produce large fruits, and that that of insufficient manure is to produce small ones, and so forth. It seems more important to show that the number of ray-florets can either be increased or diminished by selection: but even on this point there is no doubt whatever. The only question is which of these two factors will preponderate in given instances?

[1] Part I, § 9, p. 85.

The experimental part of the work is to provide the nutrition, i. e., generally favorable conditions of cultivation. The results, however, have to be dealt with by statistical methods which were originated by QUETELET and GALTON[1] and have been developed in recent years amongst others by PEARSON, LUDWIG, DUNCKER, DAVENPORT and AMANN.[2]

Let us begin with the latter point and let us seek to delineate the main features of this method in a few short paragraphs in order that we may have a clear idea of the manner in which they are employed. I have chosen GALTON's method as the simplest and most convenient for the latter purpose.

QUETELET and GALTON have shown that the individual variations of men and other animals follow the laws of probability. The deviations from the type of any fluctuating character can be expressed by a curve since they are grouped symmetrically round the type as a center of greatest density. The more numerous the observations the more exactly does the curve of variability coincide with the curve of probability. The cause of this parallel is, pretty obviously, that the various deviations from the normal are determined by a vast number of external and internal influences.

QUETELET asserted that the above law applied to plants and GALTON demonstrated it by a few experiments. My cultures of races and varieties extending, as they have done, over many years, have given me plenty

[1] GALTON's *Natural Inheritance* is indispensable for a proper understanding of the foundations of this method and the reader is advised to refer to it in conjunction with this chapter.

[2] My experiments were made in 1892-1894, i. e., before the publications of these authors had appeared.

of opportunity of convincing myself of its general applicability in the vegetable kingdom.[1]

When it is once proved that the form of the empirical curve of fluctuations in plants coincides with that of the theoretical curve of probability, so far as unavoidable errors in observation permit, the properties of the latter may evidently be ascribed to the former.

The most important property of the curve for our purposes is that it may be definitely described by two magnitudes, (I) the mean value of the character in question and (II) the amplitude or extent of variation. The mean value used by GALTON is that magnitude which half of the individuals exceed, but which the other half do not attain. This he calls the median. It need not be a magnitude which actually exists, but is found by interpolation on the assumption that variation is unbroken and continuous.

GALTON'S median can be determined more easily than the ordinary mean, which is obtained by dividing the sum of all values by the number of observations. It has exactly the same justification and in symmetrical curves the two necessarily coincide.

The second factor is the amplitude of variation which finds its simplest expression in the remoteness of the extreme variants, provided that the number of individuals is not too small. But the rarity of these extremes makes the determination of these limits by their simple observation largely a matter of chance. GALTON therefore uses another value borrowed from the theory of probability, as a measure of the amplitude. This is the magnitude of the deviation from the mean which is exceeded by a

[1] See *Ber. d. d. Bot. Gesellsch.,* Bd. XII, 1894, p. 197, where the previous literature is cited.

quarter of the individuals and therefore analogous to the so-called "probable error." He calls it the Quartile (Q). There is obviously one quartile on either side of the Median (M); these are called Q_1 and Q_2. If the curve is symmetrical, the two quartiles have the same value; otherwise the dissimilarity of the empirically determined Q_1 and Q_2 is a measure of the degree of symmetry of the curve. If the difference between the two is within the range of the error of observation, their mean value $Q = (Q_1+Q_2)/2$ is the measure of the amplitude of variation of the material under consideration.

If we wish to compare the amplitude for different characters together we must reduce them to a common measure. This is done by dividing Q by M.[1]

We see therefore that Q_1, M and Q_2 are the numbers which have to be determined by observation. The form of the curve is determined by them and any differences between the curves so determined and the actual figures themselves must be ascribed to errors in observation, at any rate in symmetrical curves. The greater the number of observations which go to make a curve the smaller will these differences be.

In the following sections I shall deduce these values from the data; and use them as a basis for discussion. One advantage of this will be that it will render drawings of the curves superfluous, or at any rate only useful for the purpose of demonstration; and that it will compress the numerical material into a few figures.

A few remarks on the subject of construction of these curves (Figs. 115-118) are called for. The number of ordinates is by no means necessarily the same as the

[1] Ed. Verschaffelt, *Ueber graduelle Variabilität von pflanzlichen Eigenschaften,* Ber. d. d. bot. Gesellsch., Vol. XII, 1894, p. 350.

number of groups in the tables. This is sufficiently evident where we are dealing with continuous variations such as length. For here the unit chosen is quite an arbitrary one. For example, if I had measured the fruits of *Oenothera* accurately to *two* millimeters only (or if I had measured them in English inches), I should have had fewer ordinates; but if I had measured them to half a millimeter, I should have had twice as many. And in dealing with ray-florets we may consider units or pairs or larger groups. In fact the data may be grouped in any desired way, to suit our purposes.

The number of units to be used in the construction of a curve depends in principle on the number of individuals. If this is small, they must be made correspondingly few. In order to do this the two or three groups of figures, in the midst of which the interpolated value of *M* lies, are united to form a single ordinate; this forms the apex of the curve. We then deal with the groups to the right and to the left of it in the same way. This is the only way in which the peaks and valleys, in the curve, resulting from an insufficient number of observations can be smoothed away.

Finally, if the various curves are to be compared with one another, the empirical data must of course be reduced to percentages.

II. THE LENGTH OF THE FRUIT IN OENOTHERA LAMARCKIANA.

§ 3. CORRELATION BETWEEN INDIVIDUAL STRENGTH AND LENGTH OF FRUIT.

Let us now consider the relation between the individual strength of the plant and a character which can be conveniently studied by statistical methods; partly as an example of the method of dealing with measurements, described in the preceding chapter; and partly on account of the importance of the question itself. For this purpose I have chosen, as I indicated in the previous section, the length of the ripe fruits of our Evening Primrose (Fig. 114).

These fruits are highly variable, not only in plants treated differently but also in the various individuals of the same culture. It is not difficult, as a rule, to find among the longest ones individuals which have twice the length of the shortest ones (Fig. 114 A and C). Such fruits are however very rare; the intermediate ones (Fig. 114 B) are always by far the commonest. In sorting such material we easily find that the frequency of the various values is describable in terms of the QUETELET-GALTON law, especially when the number of plants measured is large.

Fig. 115[1] exhibits these values graphically. The measurements were made on 568 plants; and, in each case, the

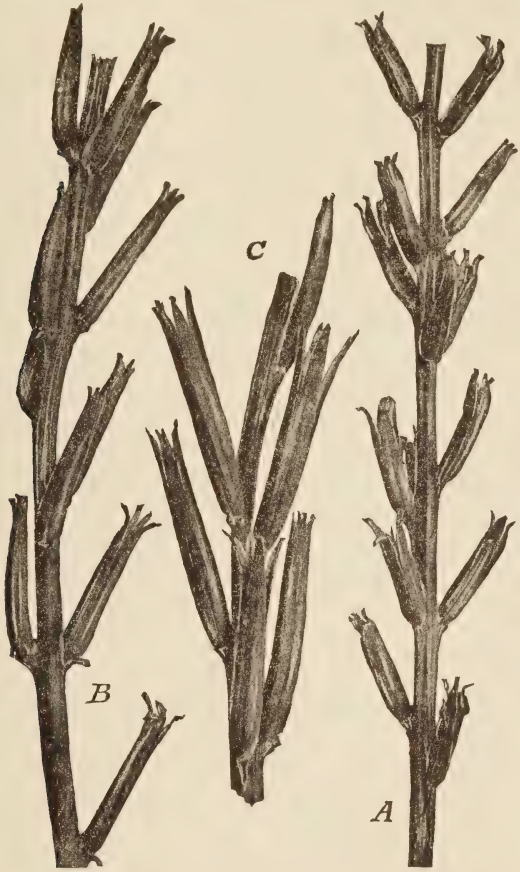


Fig. 114. *Oenothera Lamarckiana.* Lower sections of three fruit bearing stalks taken from the main stems of three plants, natural size. A, small; B, median; C, long fruits. Culture of 1899.

lowest ripe fruit was measured. The lengths of these fruits ranged between 15 and 34 millimeters, and their

[1] *Ueber halbe Galtoncurven als Zeichen discontinuirlicher Variation,* Ber. d. d. Bot. Gesellsch., Bd. XII, 1894, Table X, Fig. 1. The

mean length was 24 millimeters. They agree, as a comparison with the dotted line shows, fairly exactly with the probability curve.

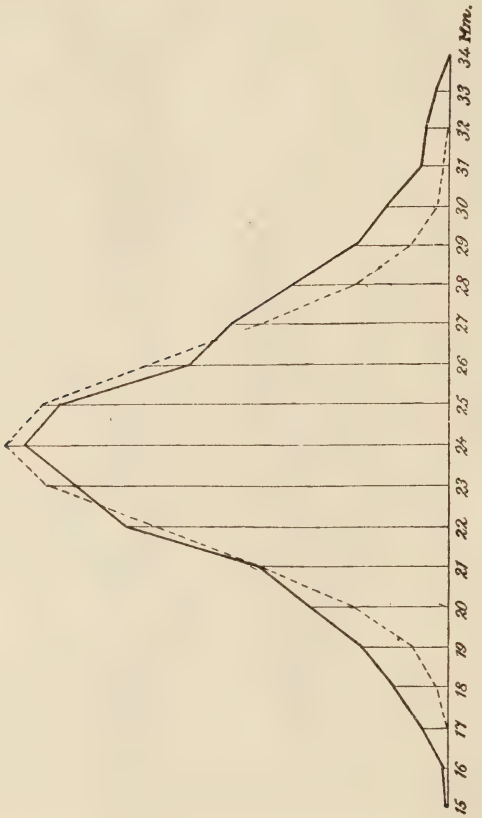


Fig. 115. *Oenothera Lamarckiana.* Curve exhibiting variation in the length of fruits of 568 plants. The dotted line is that given by the QUETELET-GALTON law. Hilversum, 1893.

If we calculate the values, which we described in the preceding paragraph, from these data we get the following, in millimeters:

Minimum	*Qo*	M	*Qp*	Maximum
15	22.2	24.1	26.1	34

data for this curve appear on page 200. This curve was the first to demonstrate the applicability of the QUETELET-GALTON law to the vegetable kingdom.

Maximum and minimum simply refer to the length of the longest and shortest fruits. M is GALTON's median or the mean—the value of which half the individuals do not attain, but is exceeded by the other half.

This median is found by interpolation, on the assumption that the fruits measured as 24 mm. varied continuously between 23.5 and 24.5 mm. Qo and Qp are the ordinates which are separated from M by a quarter of all the individuals in each case. They are also found by interpolation.

GALTON's quartiles are therefore: $Q_1 = M - Qo$ and $Q_2 = Qp - M$. Further $(Q_1 + Q_2)/2 = Q$ is the measure of the amplitude of the curve. Lastly Q/M is a measure of this value independent of the size M and of the nature of the variable character; a number therefore by means of which the variation of the fruit length in *Oenothera* may be compared with the variation of other characters in other plants.

These values calculated from the above data are as follows:

Q_1	Q_2	Q	$\frac{Q}{M}$
1.9	2.0	1.95	0.08

In the description of the experiment Qo and Qp can be omitted, now that the values Q_1, M and Q_2 have been calculated from the empirical data.

A greater degree of accuracy can be attained in these investigations by determining the mean length of the fruits on a given plant instead of determining that of a single fruit only. The question then arises: from how many fruits should this mean value be calculated. I have measured five; and in this section and in the following one I have used the mean of the lengths of the lowest

five good fruits as a measure of the length of fruit in each individual.

The reasons which led me to this choice are the following. My selection was always an individual one; that is to say I did not search for the longest and shortest fruits in the harvest, but for the individuals the mean of whose fruits was the longest. and for those the mean of whose fruits was the shortest. But on each inflorescence the size of the fruits gradually decreases from below upwards with the gradual exhaustion of the plant. Lateral branches often have small capsules; but as a rule I did not allow these to develop; I simply broke them off quite young. For that was the only way in which it was possible to grow a large number of healthy plants on the relatively small space at my disposal.

The mean length of the five lowest fruits is obviously more or less an arbitrary measure of the mean length of the fruit of a plant. It would be more accurate to measure ten or twenty fruits. We cannot count, with sufficient certainty, on more than twenty ripe fruits per plant; many individuals do not bear so many; for the flowers which open after the first of September usually do not ripen their fruits with us. To measure the mean length of *all* the fruits on a plant, *all* the lateral branches would have to flower, and measurements would have to be made of the ripe fruits of *all* the flowers. But this is absolutely impossible; at least in our climate, and when the plants are cultivated as annuals.

Fortunately the measurements of the five lower fruits gives figures the accuracy of which is sufficient for our experiment. In order to prove this statement by a direct experiment I took 38 plants in November 1893 and meas-

ured the mean length of the lower five and of the lower twenty fruits on them.

The mean length of the fruits is found by dividing the sum of their lengths by the number of fruits measured. For this purpose the fruits were cut through just at their base (which is marked at its point of junction with the bract by a constriction, so that the measurements could always be taken from a fixed point), laid one after another, end on end, in a row, great care being taken in arranging them; and the length of the whole series was read off. In this way a greater exactitude of the measurements is attained, whilst only one measurement is necessary for each plant.

Let us choose an example. On one plant the total of the lengths of the five lower fruits was 167 mm., that of the twenty lower fruits 688. The mean numbers were therefore 33.4 and 34.4. The difference is 1.0 mm.

In this way the differences for the 38 plants were determined; some were positive, others negative. Neglecting the sign the differences were now written in a series in order of magnitude. The result was that in half the individuals the difference was less than 1.25, but in the other half greater. In one case only did it reach as much as 4 mm. The probable error is therefore 1.25.

In other words: In the highly improbable case of all the differences being positive, or all negative, the figures in our table would have been 1.25 mm. more accurate if I had always measured 20 instead of 5 fruits. Differences of 1.25 and less must therefore be regarded as within the limits of errors of observation. The differences occurring in the experiments to be described are, as

a matter of fact, almost without exception considerably larger.

With a view to studying the correlation between individual strength and length of fruit[1] I also measured, on the same 38 plants, the length and thickness of the stem and the thickness of the fruits. The thickness of the stem was measured just above the root and round the lowest fruit-bearing internode. The length of the stem was complicated by other factors; the plants which came up late were abnormally elongated because the light was kept off them by their taller neighbors. I shall therefore not deal further with this character.

The data are summarized in the table below. This has

CORRELATION BETWEEN THICKNESS OF STEM AND LENGTH OF FRUIT IN OENOTHERA LAMARCKIANA.

THICKNESS OF STEM		MEAN THICKNESS OF FRUIT	MEAN LENGTH OF FRUIT	NUMBER OF INDIVIDUALS
BELOW	ABOVE			
16	12	3.85	38.6	2
15	9	3.5	35.0	2
14	9	3.7	31.8	2
12	8	3.5	34.1	3
11	9	3.2	30.2	2
11	8	3.3	32.7	2
11	7	3.4	31.6	3
10	8	3.1	31.9	2
10	7	3.0	30.6	9
9	7	2.9	29.2	2
8	7	3.1	29.7	3
8	6	3.0	29.9	3
7	5	3.1	30.1	3

[1] The method of measuring and estimating correlations between variable organs was originated by GALTON. See *Correlations and their Measurements.* Proc. Royal Soc., Vol. 45, (1888), p. 135. See also GALTON, *ibid.*, Vol. 40, p. 42 and WELDON, *ibid.*, Vol. 51, (1892), page 3.

been condensed by uniting the individuals with similar thickness of stem, and by giving the mean length of their fruits. The number of individuals per group is given in the last column. The length and thickness of the fruit was measured on the lowest 20 fully developed fruits in the case of each individual in the manner described above. All the values are expressed in millimeters.

The table brings out the strong correlation existing between thickness of stem and thickness and length of fruits. For, apart from negligible individual differences, the fruits are longer and thicker, the thicker the stem is. These figures are not sufficiently extensive for the determination of GALTON'S value r;[1] but they serve their immediate purpose well enough.

Taken in conjunction with the rest of what we know about nutrition and growth in our plant they tell us that as a rule the fruits are longer, the more vigorous the plant is, and especially that the longest fruits are only found on the strongest plants. Selection in the direction of long fruits therefore chooses the strongest plants whilst selection in the opposite direction must choose the weakest.[2]

It should be mentioned here that manuring and the choice of good seed are not the only methods of ensuring the vigor of a plant. The distance of the plants from one another, especially in youth, plays a very prominent part in determining this. Plants standing alone usually grow up very luxuriantly; the more plants one grows per square meter the less vigorous are they. Another method of effectively increasing the individual strength of the

[1] r = ratio = measure of correlation.

[2] It will be seen that this generalization agrees perfectly with the considerations set forth in the critical part of this work. Cf. in this respect, *Papaver somniferum polycephalum*, pp. 137-140.

plant—the culture of seedlings in pots— will be described in the next section.

§ 4. THE SIMULTANEOUS OPERATION OF NUTRITION AND SELECTION.

The length of the fruits of the large-flowered Evening Primrose (Figs. 114 and 115) will afford suitable

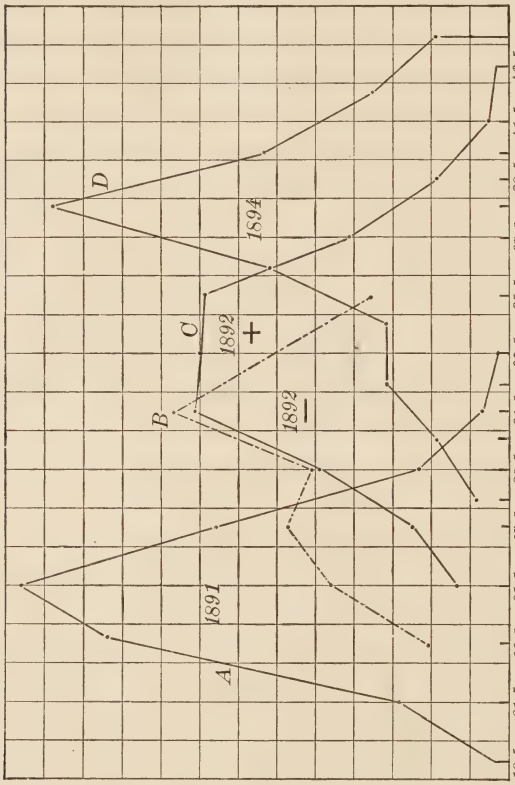


Fig. 116. *A, B, C, Oenothera Lamarckiana.* Shifting of the variability curves by selection and nutrition. Graphic exhibition of the tables in this section. Curve *D, Oenothera rubrinervis*, exhibits the result (described in the following section) of high nutrition without selection. The figures under the abscissae are the mean fruit-lengths in millimeters.[1]

material with which to gain an insight into the interaction between nutrition and selection. With regard to nutrition

[1] The curve is constructed from the tables given in the text by reducing the number of ordinates to one-half. All figures are con-

I have confined myself to positive changes, but with regard to selection to both positive and negative ones; and I have also studied the effect of high nutrition continued through a number of generations without selection.

High nutrition has proved itself superior to the most stringent selection (Fig. 116). Even when combined with negative selection it has improved the mean (Fig. 116 B) and positive selection has, in combination with it, only been able to achieve very little more (Fig. 116 C). And without any selection at all an exceptionally high nutrition has had a far better result than the first two combinations (Fig. 116 D).

Fig. 116 shows the main result of this whole series of experiments. The curves B (negative selection) and C (positive selection) are taken from the first year; this was done because the two following years brought no further progress in the same direction in spite of continued selection. The experiments extend over three generations; but all nine curves have not been included since this would have rendered the figure practically unintelligible.

For this experiment, seeds of the *laevifolia*-family (p. 273) were sown in 1891 and some of them highly manured with horn-flour (steamed and crushed horns

verted into percentages. The distance of the ordinates apart is 7.5 mm. The height of the ordinates is 1% = 2 mm.

A. (123 plants) The original curve of the mean fruit-length after the first application of nitrogenous manure in 1891.

B and *C.* The result of manuring the mother-plant in 1891.

B (78 plants) The next generation after selection of short-fruited seed-parents. The curve has nevertheless shifted distinctly to the right. 1892.

C. (147 plants) The same generation as *B*, but after selection of long-fruited seedparents; the curve has only shifted a little more than *B*. 1892.

D. After three years of cultivating the seedlings in pots, i. e., by the most effective form of nutrition, but without selection. The curve has shifted to the right far more than *C*. 1894 (88 plants).

and hoofs). One plant with very long fruits and two with very small fruits were chosen from the harvest, after its curve (Fig. 116 A) had been determined. Their seeds were sown separately in 1892 and moderately manured; the curves of their offspring were determined.

The result was, as Fig. 116 shows, that the length of the fruit had increased in both cases. We see that this occurred in spite of the choice of short-fruited seed-parents in one-half of the experiment. The effect of manure therefore exceeded that of selection (Fig. 116 A, B, and C).

HARVEST OF 1891.

MEAN LENGTH OF FRUIT IN MM.	NUMBER OF PLANTS	
	WITH HORN-MANURE	WITHOUT HORN-MANURE
20	1	0
21	4	0
22	7	0
23	11	5
24	21	5
25	25	10
26	20	8
27	14	10
28	10	11
29	3	4
30	4	5
31	1	4
32	1	3
33	1	4
34	0	2
Totals	123	71

To go into the details of the experiment: it must be related that the family in question (1887-1890) was grown in very rich soil but without manure. I selected

at random two samples of seed, each of which had been well mixed, from those harvested in 1890. One was sown on two beds of about 2 square meters each; which had received a dressing composed of 5 kilos of horn-flour, and 10 kilos of this manure per square meter respectively. This culture gave 123 healthy plants with ripe fruits. The greater part of the seed was sown on five beds, of 2 square meters each, some of which received no manure at all, whilst others were given ½ to 2½ kilos of ordinary guano per square meter. Of this crop 14-15 plants were chosen at random from each bed and employed for determining the second curve.

The total length of the five lower fruits was measured in millimeters (see p. 532) and the mean length of fruit calculated from this.

In this way I obtained the data in the table on p. 538.

The following figures can be calculated from the first generation of this experiment, raised from the same lot of seeds:

	Q_1	M	Q_2
With horn meal	1.3	25.2	1.5
Without horn meal	1.9	27.2	2.4
Hilversum	1.9	24.1	2.0

In the third row I have written the corresponding values for *O. Lamarckiana* (1893), for the sake of comparison (see pp. 530, 531 and Fig. 115).

The cultivated plants have, it will be seen, a slight advantage over the wild ones, which is smaller in the case of the plants which had horn-flour than in those in the control experiment. The horn-flour culture shows a slight decrease in the amplitude of variation; the control experiment a trifling increase.

The horn-flour culture was the only one which was

continued. Three individuals from it were chosen as seed-parents; the mean lengths of their five lowest fruits measured as above were 20.6, 20.6 and 32.6. For the sake of greater certainty I also measured all the ripe fruits on these stems (27-33 fruits each) and found the mean values for the plants to be 19.0, 19.2 and 31.3. The seed of the single long-fruited stem was sufficient for the culture of 1892; but I had to take two of the short-fruited ones to get a sufficient quantity of seed.

HARVEST OF 1892.

MEAN FRUIT LENGTH IN MM.	NUMBER OF PLANTS	
	K	*L*
23	2	0
24	2	0
25	4	0
26	5	5
27	7	5
28	12	4
29	5	8
30	5	10
31	5	17
32	12	13
33	6	13
34	6	16
35	5	16
36	2	13
37	0	5
38	0	10
39	0	6
40	0	1
41	0	2
42	0	0
43	0	3
Totals	78	147

In 1892 I set apart a bed of 4 square meters for each

of these two cultures: it was dressed with ⅓ of a kilo of dried cow manure, and ⅙ of a kilo of steamed horn-flour per square meter. This has proved the most satisfactory manure I have tried: plants do not react, in the long run, to larger quantities.

Otherwise the treatment of the plants was the same as in the former year; they grew healthily; there were 147 individuals from the long-fruited parentage, and 78 from the short-fruited. The fruit lengths were determined in the usual way; and the number of plants which exhibited the various fruit-lengths are given in the table on page 540, in which K signifies the offspring of short-fruited and L that of long-fruited parents.

From the table on page 540 together with result of the sowing of 1891 the following values can be calculated: under S are given the fruit lengths of the seed parents.

	S	Q_1	*M*	Q_2
Harvest of 1891	—	1.3	25.2	1.5 (Fig. 116 *A*)
1892. Short fruited culture	20.6	2.5	29.9	2.6 (Fig. 116 *B*)
1892. Long fruited culture	32.6	2.6	33.4	2.4 (Fig. 116 *C*)

and further:

	MINIMUM	MAXIMUM
Harvest of 1891	20 mm.	33 mm.
1892. Short fruited culture	23 mm.	36 mm.
1892. Long fruited culture	26 mm.	43 mm.

We find therefore that the mean fruit-length has increased considerably in both cultures of 1892, and that this increase has been more considerable when long-fruited seed-parents have been chosen than when short-fruited ones have. The same is true of the extremes of the crops: fruits as small as those which occurred in 1891 did not occur in the cultures of 1892: on the other hand the size of the longest fruits increased consider-

ably (the maximum increase being almost a third of the original length).

For the sake of further discussion, we may sum up this result briefly in two theses:

1. In both cases the length of the fruit increased.
2. With the selection of a long-fruited seed-parent this increase was considerably greater than when a short-fruited one was selected.

It is evident that the latter fact is simply the result of selection. All the other conditions of the experiment were exactly the same, and the difference in the results is exactly what one would expect as the result of selection. We need not therefore enter further into it.

But it is a very different matter that the length of the fruit increased in both cultures and especially that this happened in the case of the choice of short-fruited seed-parents. This cannot have been the result of selection, and the only other possible cause can have been the heavy manuring of the parent-plant with horn-flour.

In the long-fruited culture the mean fruit-length (33.4 mm.) was larger than the corresponding value in the seed-parent (32.6 mm.). The known principles of selection, and particularly GALTON's researches on regression, make the interpretation of this result as the effect of selection, impossible. Selection would, of course, effect an increase in the length of the fruit, but the new value would have to lie between the original mean and the fruit-length of the seed-parent. Here however it was greater than that of the seed-parent, and this can only be ascribed to the heavy manuring of the parent-plants.[1]

[1] I have often observed this effect of the manuring of the parent-plants in cultures with other species, for example in *Ranunculus bulbosus* in pleiopetaly. See the second volume.

Let us now turn to the amplitude of variation (Q). This was, as the above table shows, the same in both cultures in 1892 and double as large as in the horn-flour culture of 1891. In this latter it was, in fact, smaller than in the ordinary cultures (p. 539). The amplitude of fluctuation is well known to be brought about by the multiformity of internal and external conditions which affect development, and it is obvious that heavy manuring will tend to level these differences down. We shall refer to a parallel result when we come to describe the continuation of the short-fruited race.

Finally, it will be seen that Q_1 and Q_2 have remained equal to one another and therefore that the curve, in spite of the shifting of its apex, has remained symmetrical.

Regarded from the methodological point of view, this experiment contains a warning to keep the external conditions, particularly those of manuring, as constant as possible; and not to be too ready to interpret any changes that may occur as the effects of selection.

As already stated I have cultivated the two races for two more years under exactly the same treatment (1893, 1894). The long-fruited race underwent no further improvement; in fact they deteriorated a little. This result is an illustration of HALLETT's principle (see p. 110), which enabled him to evolve his new varieties of cereals. During the first year of his experiments notable progress was made; but after that, further selection either made very slight further progress, or only served to fix what had already been attained.

In 1891-1892 I left pollination to the agency of insects, but in the summer of 1893 I pollinated the flowers artificially after having excluded the visits of insects by bags. But this has not led, so far as I have observed,

to any considerable difference in the results. The significance of free crossing by insects is usually very much exaggerated. The pollination of the evening primrose is chiefly done by humble-bees; although *Plusia gamma, Agrotis segetum* and allied moths participate to a small extent in my garden. These insects, especially the humble-bees, usually visit all the flowers on the same stem one after the other, so that there is a great amount of self-fertilization taking place.

In 1892 I placed the separate cultures at some distance from one another, and separated them by brush wood, so that frequent crossings between them were practically impossible. Artificial pollination in these experiments has the great disadvantage that one has to choose the seed-parents whilst they are in flower, that is to say, a long time before the full development of their fruits; the choice is therefore not nearly as free as when pollination is left to insects.

The following description of my experiments shall be condensed as much as possible. I shall begin with the long-fruited race.

The seed-parents in 1892 were two plants with a mean fruit-length of 42.6 to 43.0 mm. The seed-parents in 1893 were three plants whose mean fruit-lengths were 37.0, 37.0 and 41.0. In the first year therefore there was a considerable advance on the fruit-length of the plants chosen in 1891 (32.6); in the second year however a slight retrogression which was brought about by the necessity, referred to just now, of carrying out the selection before the fruits were ripe.

The crop in both years was dealt with and measured in exactly the same way as in 1892. There resulted the

following numbers of individuals of the various mean fruit-lengths given in the first columns below.

LONG-FRUITED RACE IN THE YEARS 1893 AND 1894.

MEAN FRUIT LENGTH IN MM.	NUMBER OF PLANTS	
	1893	1894
23	0	2
24	1	3
25	3	2
26	5	2
27	7	9
28	6	8
29	15	9
30	12	8
31	15	6
32	11	11
33	14	9
34	10	14
35	10	6
36	6	5
37	5	3
38	2	1
39	0	1
40	2	1
41	1	1
Totals	125	101

The values Q and M calculated from the above table are given below; together with the corresponding values for the ancestors, of 1891 and 1892, and the lengths of the fruits of the individual plants which furnished the seeds (S = seed-parent). There stands therefore under S in each row the length of the fruit of the seed-parent chosen in the preceding autumn; their seeds gave rise to the crop referred to in the same line.

	S	Q_1	M	Q_2
Harvest of 1891	—	1.3	25.2	1.5
" " 1892	32.6	2.6	33.4	2.4
" " 1893	42.6—43.0	2.3	31.4	2.6
" " 1894	37.0—41.0	3.2	31.6	2.4

The mean fruit-length has therefore, in spite of rigid selection not only not increased but actually decreased. Selection can do no more than, to use HALLETT's expression, fix the fruit-length attained by high nutrition: and it barely manages that.

The quartiles have remained pretty constant since 1892; the curve has remained practically symmetrical and its amplitude has neither increased nor decreased much.

The increase in the mean fruit length was effected (in 1892) without any regression; but after that the selection was accompanied by a heavy regression; that is to say, the value of M, reached in the years 1893 and 1894, fell far short of the M of the selected seed-parents (S).

* * *

We now come to the continuation of the short-fruited race in the two years 1893-1894.

Like the long-fruited culture, this was continued for two more years under normal conditions of manuring and by selecting seeds from very short-fruited plants, for raising the next generation. In § 3 it was shown that short-fruited plants were as a rule ill-favored, i. e., poorly nourished ones. In this way selection would very soon counteract the effect of the heavy manuring of 1891. And the mean fruit-length has, as a matter of fact, undergone a marked diminution in these two years, whereas the amplitude of variation has, on the other hand, increased considerably.

The culture extended in 1893 over four and in 1894 over six square meters, manured with dried cow manure and horn-flour as before. Two plants with mean fruit-lengths of 23.2 and 23.4 mm. were chosen to supply the

SHORT-FRUITED RACE IN THE YEARS 1893 AND 1894.

MEAN FRUIT LENGTH IN MM.	NUMBER OF PLANTS	
	1893	1894
16	1	0
17	1	1
18	4	2
19	4	3
20	2	11
21	9	12
22	13	12
23	8	11
24	7	10
25	11	5
26	9	8
27	15	4
28	9	2
29	9	8
30	7	4
31	10	7
32	13	6
33	1	4
34	2	3
35	0	0
36	2	4
37	1	1
38	0	0
39	1	0
Totals	139	118

1893 crop. In this year the short-fruited plants afforded so little seed, partly on account of the small number of artificially fertilized flowers, that seed of six plants had to be harvested to provide a sufficient quantity (8.6 ccm).

The mean fruit-lengths for these six seed-parents were 15.6, 17.0, 18.2, 19.2, 20.2 and 21.4; the average of which is 18.6 mm.

The fruit-length of the seed-parent chosen in 1891 was 20.6; from which we see that the above figures are nothing more than fluctuations round a similar mean.

The harvest was again treated in the same way; the mean fruit-length was determined for each plant from the total length of the lowest five good fruits: in the table on page 547 are given the numbers of individuals exhibiting the various lengths written in the column to the left.

Here are the values calculated from this table; together with those of their ancestors and of the seed-parents (S) chosen each year.

	S	Q_1	M	Q_2
Harvest of 1891	—	1.3	25.2	1.5
" " 1892	20.6	2.5	29.9	2.6
" " 1893	23.2—23.4	3.9	26.5	3.3
" " 1894	15.6—21.4	2.7	24.2	5.2

These figures show that the mean fruit-length decreased about as much, as a result of thrice repeated selection, as they had increased in 1892 as the result of the heavy manuring of 1891. Regression took place, as was to be expected, in the two years covered by the experiment. The amplitude of variation exhibited a marked increase in this experiment; the external and internal causes affecting the growth of a plant are obviously multiplied by the choice of ill-favored individuals under favorable conditions of cultivation. In other words: selection and cultivation exert their influence in opposite directions in this case, whereas in the long-fruited race they exerted it in the same direction; hence the ampli-

tude of variation $\left(Q=\frac{Q_1+Q_2}{2}\right)$ increases in this case but not in the former.

In connection with this result, there are two further points relating to the selection of continuous variations.

In the first place both agricultural and horticultural selection is usually accompanied with moderate manuring, and the most desirable individuals are usually found amongst the strongest ones. Inasmuch as we have here a contrast similar, though working in the reverse way, to that which obtains in our experiments, we may expect an increase in the amplitude of variation as a result of this contrast.

In the second place if I had mixed the two races in 1894, or if I count the figures in the tables on pp. 545 and 547 together and calculate Q_1, M and Q_2, from the whole lot I get (for 118+101=219 plants):

	Q_1	M_1	Q_2	$Q=\frac{Q_1+Q_2}{2}$
1894	5.0	28.6	3.8	4.4

whereas Q for the short-fruited race alone was

$$\frac{2.7+5.2}{2}=4.0.$$

That is to say, the amplitude of variation is so much increased by the opposite action of nutrition and selection, that it can only very slightly increase further by lumping the extreme variants in both directions together. In other words Q (in the case before us) is increased far more by the changing conditions of nutrition in the individual plants on the same bed than it can be by selection in two opposite directions.

Summary. I append the values for Q_1, M and Q_2

derived from the above experiments, collected in a single table. The numbers signify millimeters as before.

FRUIT LENGTH OF OENOTHERA LAMARCKIANA.

	Date	S	Q_1	M	Q_2
Original form, Hilversum	1893	—	1.9	24.1	2.0
" " culture	1891	—	1.3	25.2	1.5
Long fruited race	1892	32.6	2.6	33.4	2.4
" " "	1893	42.6—43.0	2.3	31.4	2.6
" " "	1894	37.0—41.0	3.2	31.6	2.4
Short fruited race	1892	20.6	2.5	29.9	2.6
" " "	1893	23.2—23.4	3.9	26.5	3.3
" " "	1894	15.6—21.4	2.7	24.2	5.2

I regard the following generalizations as the most important results of these experiments, combined with the results detailed in the next section (Fig. 116 D):

1. The variation of the length of the fruit follows the QUETELET-GALTON law (Fig. 116 A-D). Each curve is determined by three values. The median, M, or the mean value, and the two quartiles Q_1 and Q_2 within which fall half of the deviations from the mean.

2. The mean fruit-length is much influenced by nutrition as well as by selection, and more by a single manuring of the parent-plant than by a once or twice or even thrice repeated selection of long-fruited plants as seed-parents (long-fruited race 1891-1894). It is influenced even more by a few years of cultivating the seedlings in pots, and the addition of much manure to the pots of the seedlings (pot-culture without selection 1892-1894, § 5).

3. The amplitude of variation $\left(Q=\frac{Q_1+Q_2}{2}\right)$ increases only slightly, so long as nutrition and selection work in the same direction. But as soon as they work in opposite directions the multiformity of affecting causes in-

creases, and the amplitude of variation increases too (short-fruited race 1891-1894).

4. The variability-curves remain almost symmetrical ($Q_1 = Q_2$) although their apices are considerably shifted to one side. The deviations from this symmetrical form almost all lie within the limit of ordinary errors of observation.

§ 5. THE SHIFTING OF THE CURVES OF VARIABILITY BY NUTRITION.

Oenothera Lamarckiana, and other plants as well, may be stimulated to a much swifter and more vigorous growth by planting the seeds in pans and picking out the young seedlings soon after the unfolding of the cotyledons into fairly large pots filled with heavily manured garden soil. One would expect that, by continuing this process for a few generations, it would be possible to increase the mean fruit-length very considerably, in accordance with the principle of nutrition of the parent-plant.

The experiment to be described fulfils this expectation; the increase made in three years (1892-1894) far exceeds that made in the selection experiments already described, in which the seed was sown in the garden (Fig. 116).

Let us give a description of this experiment year by year. It began in the spring of 1892 with the seeds of the species *Oenothera rubrinervis* (p. 273) which arose in my experimental garden in 1889: the length of the fruit in this species is the same as in *O. Lamarckiana* (Fig. 99, p. 446).

In 1890 the seeds were harvested from a number of

plants without any attention being paid to their fruit-length; in 1891 however the plants with short fruits were weeded out before they ripened their seed. The seeds of the remainder were mixed and sown in wooden boxes, in February, in the greenhouse belonging to my laboratory. As soon as the cotyledons were fully unfolded a number were planted out singly in pots of 9-10 centimeters in diameter without any regard to differences in development (which as a matter of fact at this stage are scarcely appreciable). The soil was a good leaf mould, to every litre of which was added 10 grammes of dry powdered cow manure and 10 grammes of horn flour, a very strong dressing which I have used with the best results for producing contortions, fasciations and other structural abnormalities.[1] The young plants were at first kept under glass until the rosettes were very strong and had begun to develop a stem. At the end of May they were planted out in my experimental garden in a bed far removed from the other cultures. As in the latter the plants were deprived of all their lateral branches, so that they flowered only on the main stem.

Thanks, doubtless, to the early sowing and to accelerated early growth this culture flowered some weeks earlier than the others; they also ripened their fruits considerably earlier. I had altogether 22 plants whose seeds were harvested separately. Of these I chose five for next year's sowing after harvesting time was well past, and the fruits were no longer at hand. In this way no regard could be paid to the fruit-length of the seed-parents which had not even been measured.

Next year (1893) the seed was sown in the middle

[1] *Eine Methode Zwangsdrehungen aufzusuchen*; Ber. d. d. bot. Gesellsch., Bd. XII, 1894, p. 25.

of March in exactly the same manner as described above; as soon as the seedlings had fully unfolded their cotyledons they were planted out into the same compost as in 1892, and treated in the same way subsequently. Towards

CULTURE OF THE SEEDLINGS IN POTS; OENOTHERA RUBRINERVIS.

MEAN FRUIT LENGTH IN MM.	NUMBER OF PLANTS	
	1893	1894
24	2	0
25	2	0
26	2	0
27	4	0
28	5	1
29	5	1
30	7	1
31	10	3
32	15	2
33	7	5
34	2	2
35	7	5
36	1	4
37	0	10
38	0	10
39	0	16
40	0	7
41	0	9
42	0	7
43	0	1
44	0	4
Totals	69	88

From which the following values have been calculated for Q_1, M, Q_2:

Pot-culture	Year	Q_1	M	Q_2	Min.	Max.
2nd generation	1893	2.2	31.2	1.3	24	36
3rd generation	1894	2.5	38.3	2.2	28	44

the end of September I had 69 plants with ripe fruits. Their lengths were measured in the usual way on the lowest five good fruits; and the figures thus obtained are given in the 1893 column of the table on page 553.

I now had to make a sowing without reference to fruit-length. I sowed the seeds of nine plants whose mean fruit-lengths were 24.2, 26.2, 26.8, 27.0, 27.4, 29.0, 32.4, 34. 6, 35.2 mm. The mean of them was therefore 28.1 mm., which is below the median of the whole 1893 crop (see below) whilst only the last two figures lie above the upper quartile.

Sowing, pricking out, manuring and cultivation were the same in 1894 as in the previous years. At harvest time I had 88 plants with ripe fruits; from 7 to 19 from each parent plant, with the exception of the three parents with the longest fruits which gave rise to only 4, 5 and 6 plants respectively, whereby their effect on the curves was diminished considerably. The measurements of the mean fruit-lengths were again made in the same way.

The numbers of individuals in the various groups of fruit-lengths are given in the table on page 553.

The mean fruit-length has, it will be seen, increased considerably: this is also well seen by looking at curve D in Fig. 116 and comparing it with the corresponding curve for *O. Lamarckiana,* a perfectly legitimate proceeding inasmuch as both species exhibit the same length of fruit under similar circumstances. The greatest length attained in the experiments with *O. Lamarckiana* was 33.4 which was reached by manuring the parent plants sown in the garden, and by the selection of the longest fruited plant as seed parent.

This enormous increase holds good not only for the mean but for all individuals. For the amplitude of

variation (Q_1, Q_2) has not increased very much, and is in fact a little less than in the experiments with selection. Accordingly, the minimum and maximum have been shifted in a most striking way in the same direction: small fruits are absent after three years of pot-culture of the seedlings, whilst the longest fruits have increased greatly in length.

III. CURVES OF RAY-FLORETS OF THE COMPOSITAE AND OF RAYS OF UMBELS IN THE UMBELLIFERAE.

§ 6. THE OBLITERATION OF THE EFFECT OF SELECTION BY NUTRITION.

We must now inquire whether the conclusions arrived at by our study of the fruit-lengths of *Oenothera Lamarckiana* apply to other species and other characters as well. I propose to confine myself to a single case—the operation of nutrition and selection in opposite directions, a case exactly parallel to that studied in the short-fruited race of *Oenothera Lamarckiana*. The effect of selection is pretty accurately known; so that the separate effects of selection and nutrition can be directly inferred from the result of such an experiment. It is a question of the effect of selection in a *minus* direction; of how a character will behave when we try at the same time to impair it by selection, and improve it by nutrition.

To make the significance of the point at issue still clearer I will give a short summary of the results detailed in this and the two following sections. They show that under the above conditions of experiment the effect of nutrition exceeded that of selection in *Anethum graveolens* (§ 6), that in other cases both had about the same effect, as in *Chrysanthemum segetum, Corcopsis tinctoria,* and *Bidens grandiflora* (§ 7), and finally that

in *Coriandrum sativum* and *Madia elegans* selection had decidedly a greater effect (§ 8). Thus we see that in such experiments selection and nutrition are factors of the same order, and therefore that, in breeding experiments on the effect of one of these factors, the first condition, although it is often extremely difficult to fulfil, is that the other factor should be kept perfectly constant.

The characters whose variation I investigated were the number of rays in the umbels of *Anethum* and *Coriandrum,* the number of ray-florets in the heads of *Chrysanthemum, Coreopsis, Bidens* and *Madia.* The numbers of these vary pretty considerably, and afford beautiful illustrations of QUETELET's law,[1] as will be seen at the first glance at our figures. For the construction of the curves, the numbers of rays on the terminal umbel or head of the main stem was taken as a measure of this character in the individual in question; no attention was paid to the lateral umbels and secondary heads. Seed was gathered without regard to the qualities of these lateral umbels and heads; except that those plants whose secondary or tertiary umbels or heads remained too much behind the primary one, were always the first to be rooted out.

The experiments began in the spring of 1892. The seed for sowing was obtained either from nursery-men or from botanical gardens (*Chrysanthemum*). It must therefore have been obtained from moderately manured cultures, and was sown by me in rich but not too heavily manured soil, in the open. During the three years of the experiment the manuring and other treatment was uniform. The manure was the same as that which was

[1] *Ber. d. d. bot. Ges.,* Bd. XII, 1894, p. 200. (*Coreopsis* and *Anethum*).

given to the *Oenotheras* in the same year, that is, ⅓ Kilo of dried cow manure and ⅙ Kilo of steamed horn flour, per square meter. This mixture was spread over the beds as uniformly as possible a few days before sowing and well dug in. I considered the much richer horn flour manure which I had given to the *Oenotheras* in 1891 as superfluous for this experiment.

This constant high nutrition supplied during the three years of the experiment would lead us to expect a progression of *M*; and the selection a retrogression of *M*.

I chose as seed-parents the plants with the smallest number of rays in the primary umbel or head. In the *Umbelliferae* this could be counted before the plants flowered and, inasmuch as the remaining plants were pulled up before the selected seed-parents began to flower, crossing could be prevented. The composites on the same bed did not flower all at once; each plant was recorded as soon as its rays could be counted and pulled up if it was not wanted as a seed-parent. The possibility of crossing was thus diminished as much as possible; in addition to this, the seed-parents were, whenever possible, deprived of all the heads that were over or still flowering, as soon as the selection was finished, in order to get only purely fertilized seeds for sowing. Such cultures are often threatened by numerous pestilences and misfortunes which only too often sweep away every single seed-parent, after the others have been pulled up. For example in 1894 the experiment with *Coriandrum sativum* was thus brought to an untimely end. Occurrences of this kind led me to spare a larger series of seed-parents than would otherwise have been necessary. Occasional cross-fertilization could, of course, take place among them as a result of this. From among

them I chose, after harvest was over, as many of the best as were sufficient to supply the seed for the next sowing.

From this summary of the general arrangement of the experiment, let us proceed to the description of our selection culture with the dill (*Anethum graveolens,* Fig. 117).

For this experiment seeds were bought from the trade and sown in 1892 over 1 square meter. The crop consisted at harvest time of 56 plants. The number of rays in the umbels varied between 12 and 38 and, as a rule, in direct proportion with the vigor of the plant. Six plants with 12-16 rays in the terminal umbel were chosen as seed-parents and their seeds sown in 1893 over an area of 8 square meters. The number of plants when I came to select them was 541, and as was to be expected in so much larger a number the minimum and maximum were further apart; 9 and 43. Five plants with 10-13 rays in the terminal umbel, were chosen as seed parents which constituted a notable advance in the *minus* direction, as compared with 1892.

In 1894 the culture extended over 6 square meters and the number of plants when I came to select them was 162.

The table on page 560 gives, for each of the three crops, the number of individuals whose terminal umbel had the number of rays given in the first column.

The figures (p. 560) show that, in spite of the fact that each year plants were chosen with a markedly smaller number of rays than the mean of the group from which they were chosen, the mean number of rays clearly increased during the experiment. The better manuring had therefore more effect than the selection of weak plants.

ANETHUM GRAVEOLENS.

NUMBER OF RAYS	NUMBER OF PLANTS		
	1892	1893	1894
9	0	4	0
10	0	4	0
11	0	4	0
12	1	6	1
13	1	18	3
14	0	15	1
15	3	23	5
16	7	29	4
17	6	26	3
18	12	42	9
19	6	32	6
20	3	40	6
21	1	38	11
22	5	43	10
23	3	44	9
24	0	33	7
25	1	24	9
26	1	25	15
27	0	25	10
28	1	12	7
29	1	11	5
30	0	4	8
31	1	5	6
32	1	8	6
33	0	4	4
34	1	7	3
35	0	5	5
36	0	4	1
37	0	1	4
38	1	0	0
39	0	2	4
40	0	0	0
41	0	1	0
42	0	1	0
43	0	1	0

The following values have been calculated from this table:

	Year	Seed parent	Q_1	M	Q_2	$\frac{Q}{M}$
	1892	—	1.5	18.3	3.6	0.14
	1893	12—16	3.6	21.2	3.5	0.17
	1894	10—13	4.5	25.2	4.4	0.18
Increase	1892—1893		+2.1	+2.9	−0.1	
"	1893—1894		+0.9	+4.0	+0.9	

The amplitude of variation also increased exactly as it did in the short-fruited race of *Oenothera Lamarckiana* under similar conditions.

The value Q/M renders possible a comparison between the amplitude of variation in this case and in *O.*

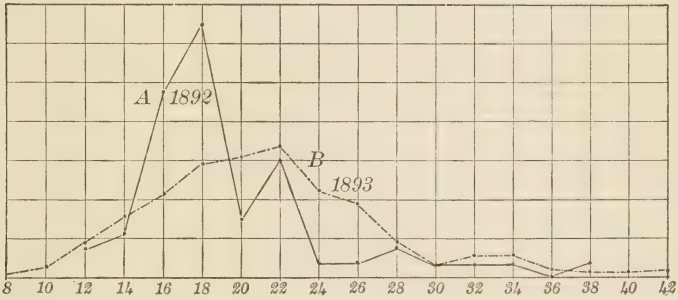


Fig. 117. *Anethum graveolens.* Curves of the rays of the terminal umbel. The numbers under the abscissae refer to the rays of the primary umbel. In accordance with the rule discussed on page 527 the number of ordinates is half the number of groups in the table. The figure 8 therefore means eight and nine rays and so forth.

A. (56 plants) Curve of 1892, irregular on account of the small number of individuals. It is also asymmetrical being drawn out more to the right.

B. (518 plants) Curve of the following generation 1893. As a result of nutrition and selection it has become nearly symmetrical.

Lamarckiana, where it was 0.08 (p. 531). The number of umbel-rays is therefore, when measured in this way, twice as variable as the fruit-length in *Oenothera.*

The asymmetrical curve of the year 1892 ($Q_2 > Q_1$)

became symmetrical in the two following years as can be clearly seen by comparing curve A (1892) and B (1893) in Fig. 117.

§ 7. EQUILIBRIUM BETWEEN THE EFFECTS OF SELECTION AND NUTRITION.

These experiments were conducted with *Chrysanthemum segetum* (Fig. 118), *Coreopsis tinctoria* and *Bidens grandiflora* (Fig. 119). Of the former I received, in exchange from botanical gardens, a certain number of packets of seeds from various sources. The contents of the various packets were mixed before sowing. This multiple origin showed itself clearly in the number of ray-florets; for the curve expressing their variation was not homogeneous as usual but had two apices (Fig. 118 A). One peak was at 13-14 florets, the other at 21. This must mean that there were two races present, mixed together.[1]

This interpretation was proved to be correct in the following year (1893) when, as a result of choosing seed-parents from one of the supposed races (the 13-rayed one) every trace of the second peak disappeared (Fig. 118 B). It did not appear again in 1894.

Two-peaked curves occur also in man, and here again they are regarded as the expression of the incomplete fusion of types which have interbred for many centuries.[2] Such curves have also been observed by Bateson[3] and Weldon[4] in their important investigations

[1] *Eine zweigipfelige Variationscurve,* Roux' Archiv für Entwickelungsmechanik, II. Band, 1895, p. 52. See also the second volume.

[2] Otto Ammon, *Die natürliche Auslese beim Menschen,* 1893.

[3] Bateson, *Proc. Zool. Soc.,* London, 1892, p. 585.

[4] Weldon, *loc. cit.*

into the variability of various animals (*Forficula, Carcinus, Xylotropus,* etc.), and repeatedly by LUDWIG in plants. BATESON, in his work on discontinuous variation, has emphasized the great importance of such cases to the student of variability, and given examples of them.[1] The two-peaked curves are separated by him as cases of dimorphism from the ordinary or monomorphic curves.

The duplicate character of curves can be brought about by the most various causes. GIARD, for example, has made the remarkable discovery that a dimorphism of this kind may be brought about when some of the individuals in a locality are infested by a parasite. Thus *Carcinus moenas* which were infected by *Sacculina carcini* or *Portunion moenadis* differed widely from the normal ones.[2]

But the double curves in plants can be dealt with experimentally much better than those in animals or men.

Let us now proceed to the description of the experiment with *Chrysanthemum segetum.* In 1892 this extended over an area of 2 square meters. The number of individuals, when I came to select them was 97. For making the curve only one head was taken from each individual, the so-called primary one at the top of the main stem. All plants whose terminal inflorescence had 14 or more ray florets were pulled up immediately; fourteen plants with 13 such florets and one with 12 were saved.

[1] W. BATESON, *Materials for the Study of Variation,* London, 1894, pp. 39-41.

Comptes rendus, T. CXVIII, 1894, No. 16 (April 16), p. 870. This case has now been thoroughly investigated by GEOFFREY SMITH, *Fauna and Flora of the Gulf of Naples.* Volume on *Rhizocephala* (Note of 1908).

In 1893 the seeds of these 15 plants were sown on 8 square meters of ground; 162 plants were raised. All of these were weeded out, with the exception of 12 plants whose terminal heads had 11-12 ray florets. That is to say, the seed-parents exhibited an advance in the negative direction as compared with the previous year.

CHRYSANTHEMUM SEGETUM.

NUMBER OF RAY-FLORETS	NUMBER OF PLANTS		
	1892	1893	1894
8	0	2	0
9	0	1	1
10	0	0	3
11	0	7	8
12	1	13	31
13	14	94	221
14	13	25	50
15	4	7	8
16	6	7	5
17	9	1	4
18	7	2	3
19	10	0	1
20	12	3	2
21	20	0	1
22	1	0	0

The curve of 1892 was therefore dimorphic; those of 1893 and 1894 monomorphic. From the two latter the following data have been calculated.

Years	Seed parents	Q_1	M	Q_2	$\frac{Q}{M}$
1893	12—13	0.4	13.1	0.6	0.04
1894	12	0.4	13.1	0.4	0.03
Increase		0.0	0.0	—0.2	

In the third year, 1894, the culture occupied 6 square meters: it was raised from the seed of three plants of 1893, each of which had 12 rays in the terminal head, and only 13 in the later ones. The number of plants at the time of selection was 338.

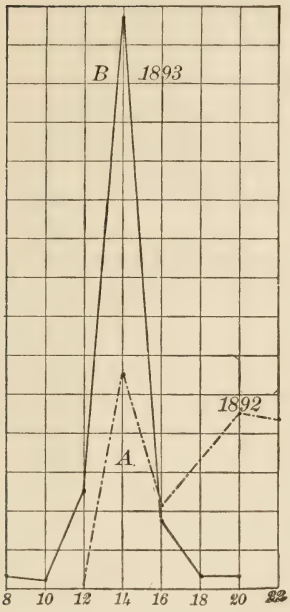


Fig. 118. *Chrysanthemum segetum.* Curves of the ray-florets of the terminal inflorescences. Under the abscissa are the numbers of these florets. The number of ordinates is reduced to the half; 8 therefore means 7-8 ray florets etc. (height: 1 mm=1%).

A (97 plants) Dimorphic curve from a mixed sowing 1892.

B (162 plants) By the selection of plants belonging to the group with 13-14 florets as seed-parents the curve has become monomorphic in the next generation, 1893. —The curve for 1894 was almost exactly the same as that for 1893.

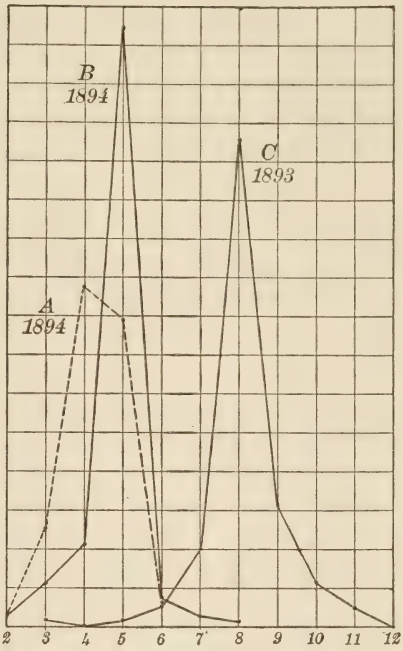


Fig. 119. A, *Coriandrum sativum* (334 plants). Curve of 1894. The numbers under the abscissa refer to the number of rays of the primary umbel. Height of the ordinates: 1 mm=1% of the individuals.

B, *Bidens grandiflora* (152 plants). Curve of 1894. The numbers under the abscissa signify, in curves B and C, the numbers of ray-florets in the primary inflorescences. Height as in A.

C, *Coreopsis tinctoria* (495 plants). Curve of 1893.

During these three years the germinating power of the seeds, and the individual strength of the whole culture increased considerably. In the first year I only got the proper number of plants per square meter by sowing a large quantity of seed; in the following year less seed was sown and the crop was correspondingly scanty: in 1894 more seed again was sown and many seedlings had to be weeded out.

The result of these observations is summarized in the table on page 564. (See also Fig. 118.)

Selection, we see, in this case has been unable to effect any further alteration in the mean or in the amplitude of variation. It has simply maintained the mean at the same point.

We come now to *Coreopsis tinctoria* (Fig. 119 C). The inflorescences of this beautiful composite have, as a rule, 8 ray-florets. Yet this number varies on the same individual as well as from plant to plant. I obtained my seeds in the winter of 1891/92 from MM. Vilmorin-Andrieux & Cie. of Paris, and tried simultaneously to increase the mean number of ray-florets by manuring, and to diminish it by selection.

The result was that the mean number maintained itself almost unaltered at 8, that is to say that the effects of the two opposing factors neutralized one another.

My cultures in the years 1892, 1893, 1894 extended over 1, 8 and 6 square meters respectively. I determined no curve for the first year; the vast majority of the plants had 8 rays; occasional ones 9 and 10; and fewer still 11, 12 or 13. These were all pulled up: I only saved a few, most of which had 7 ray-florets.

In 1893 I had 495 plants; all those which had 8 or more ray florets were pulled up as soon as the rays could

be counted, and recorded. About 60 plants with 5, 6 and 7 florets were left over. Amongst these a further selection was made of those whose branches were richest in 5-7 rayed inflorescences. Immediately after the weeding out had taken place these plants were deprived of all inflorescences which were either in flower or over, in order that all their seed might result from pure fertilization. Of the twelve plants thus treated I chose the four strongest and most fertile as seed-parents for next year's crop: their terminal inflorescences had 5, 5, 6 and 7 ray-florets respectively, and their lateral branches bore heads with few rays. In 1894 I obtained from their seeds 256 flowering plants and determined the curve from them in the usual way.

The figures I obtained are summarized in the table on page 568. (See also Fig. 119 C.)

The third experiment was carried out with *Bidens grandiflora* (Fig. 119 B). In this species the inflorescences are usually five-rayed, but the number, here also, is subject to variation and within limits similar to those in *Coreopsis*.

In the flowers of Dicotyledons the number 5 is as a general rule remarkably constant, and probably in a great many cases hardly subject to any fluctuations. The question naturally presents itself: why is this number inconstant in this case? This problem has however not yet been investigated; a solution of it would of course be of fundamental importance to the student of variability.[1]

I obtained my seeds in the winter of 1891/92 from Messrs. Haage & Schmidt in Erfurt, sowed a square

[1] The question is whether a cyclic arrangement diminishes the variability of the number of the parts involved and if so: why?

COREOPSIS TINCTORIA.

NUMBER OF FLORETS	NUMBER OF PLANTS	
	1893	1894
1	0	2
2	0	0
3	1	1
4	0	3
5	2	5
6	13	10
7	49	53
8	311	191
9	76	14
10	28	5
11	12	2
12	3	0
13	0	0

From which I have calculated the following values:

Year	Seed parents	Q_1	M	Q_2	$\frac{Q}{M}$
1893	7	0.4	8.1	0.3	0.04
1894	5, 5, 6 and 7	0.5	7.9	0.3	0.05
Increase		0.1	−0.2	0.0	

meter with them in 1892 and chose as seed-parents a few examples on which I had seen 3 and 4 rayed inflorescences.

In 1893 I sowed 8 square meters with their seeds and got 557 flowering plants; and made a curve of the numbers of rays of their primary heads. I chose a series of plants with four-rayed inflorescences and when their seeds were ripe made a further selection of three of them which had exhibited the lowest numbers of rays in their other inflorescences.

From their seeds I raised, on 6 square meters, 152 flowering individuals. I again made a curve from their

terminal heads; and found the figures given in the table on this page.

Here again as in *Chrysanthemum* and *Coreopsis* there was no marked effect on the curve while nutrition and selection were operating in opposite directions.

BIDENS GRANDIFLORA.

NUMBER OF RAYS	NUMBER OF PLANTS	
	1893	1894
2	1	2
3	10	8
4	31	16
5	355	117
6	113	6
7	40	2
8	6	1
9	1	0
10	0	0
Totals	557	152

From which I have calculated the following values:

Year	Seed parent	Q_1	M	Q_2	$\frac{Q}{M}$
1893	4	0.4	5.2	0.5	0.09
1894	4	0.3	4.9	0.4	0.07
Increase		−0.1	−0.3	−0.1	

§ 8. OBLITERATION OF THE EFFECT OF NUTRITION BY SELECTION.

The experiment was carried out partly with *Coriandrum sativum,* the common Coriander, and partly with *Madia elegans,* as species related to the oil Madia (*Madia sativa*).

The seeds of the former were obtained from MM.

Vilmorin-Andrieux & Cie. in Paris and sown on a bed of one square meter. When I came to select them the number of plants was 45; the vast majority had five rays in the primary umbel, some 6, very few 7 and 8, and none any more. Two plants had four-rayed terminal umbels, and on one of them most of the secondary umbels were also four-rayed. I only harvested seed from the two latter plants. A curve was not determined.

Next year the culture extended over two square meters, and the number of adult plants was 52. Of these the great majority had 5-rayed terminal umbels. Of the three plants which were chosen as seed-parents one had a 3-rayed terminal umbel, the two others 4-rayed ones.

The seed of these three plants was sown separately in 1894; each lot on two square meters. The number of individuals at the time of selection was 334, amongst which there occurred two with a two-rayed terminal umbel, a result which means an advance in a negative direction on the stage attained in the previous year; but may, perhaps, be partly attributed to the larger number of individuals in the culture. The plants were harvested separately on the three beds, but the results are all given together in the table on page 571. It is very curious that the offspring of the three-rayed parent exhibited on the average a greater number of rays than those of one of the two four-rayed parents. The character of the parent is therefore only an imperfect guide of the average character of its progeny.

As shown in the following table, selection has succeeded, in spite of the heavy manuring, in reducing the number of rays in the umbel by almost a whole unit.

CORIANDRUM SATIVUM (Fig. 119 A).

RAYS IN TERMINAL UMBEL	NUMBER OF INDIVIDUALS	
	1893	1894
2	0	2
3	1	43
4	8	146
5	30	133
6	12	10
7	1	0

From which I have calculated:

Year	Seed parent	Q_1	M	Q_2	$\frac{Q}{M}$
1883	4	0.5	5.1	0.4	0.09
1894	3, 4 and 4	0.5	4.3	0.6	0.13
Increase		0.0	−0.8	+0.2	

The amplitude of variation Q/M is intermediate between those of *Oenothera* (0.08) and *Anethum* (0.16).

We come now to the second series of experiments, carried out with *Madia elegans*.

This species is more suitable for experiments with selection than either *Bidens* or *Coreopsis*. In the first place the growth is much more uniform especially in youth; in the second, the number of ray-florets is considerably larger; and—last and most important point of all—there is much less partial variability in this case. This means that the various inflorescences on the same plant differ from one another only slightly in the number of their rays (at least in my race) so that the number on the terminal inflorescence can be more justly regarded as characteristic of the whole plant.

I obtained the seeds from Messrs. HAAGE & SCHMIDT in Erfurt. I sowed them in 1892 over a square meter of soil. Most of the individuals had 21 ligulate florets,

many had 20 or 22, a few had 23 or 25. These were all pulled up. There remained 6 plants with 16-19 rays; their seed was harvested in autumn.

In 1893 this experiment occupied 8 square meters. I made a curve of the ray florets of 411 plants that were raised on it. Eight plants with 13-15 florets were chosen as seed-parents.

Of these I chose the best three with 13-rayed terminal inflorescences, sowed their seeds on 6 square meters and obtained no more than 213 adult plants as a result of an accident by which a number were lost. The variability in the number of ray-florets of these plants is given in the following table, together with those of the 1893 crop.

MADIA ELEGANS.

NUMBER OF RAY-FLORETS	NUMBER OF PLANTS	
	1893	1894
12	1	0
13	15	12
14	11	16
15	18	18
16	18	20
17	43	29
18	63	32
19	101	50
20	82	23
21	54	12
22	5	1
Totals	411	213

From which I have calculated the following values:

Year	Seed parent	Q_1	M	Q_2	$\frac{Q}{M}$
1893	16—19	1.5	18.9	1.1	0.07
1894	13	2.1	17.9	1.3	0.09
Increase		0.6	—1.0	0.2	

That is to say a definite though slight decrease in the mean number as the result of fairly rigid selection.

§ 9. SUMMARY.

In conclusion, I will give the results described in the last three sections in a short summary.

The general result is that they are in complete harmony with those obtained with *Oenothera Lamarckiana* and *O. rubrinervis* (§§ 4-5) and can therefore be regarded as a confirmation of these.

They show that when nutrition and selection are brought into conflict, in some cases one of them triumphs, and in others the other. In *Anethum* it was nutrition, in *Coriandrum* and *Madia* selection, in *Chrysanthemum, Coreopsis* and *Bidens* it was a drawn battle. The differences between the results of the individual experiments has evidently more to do with the relative power of these two factors than with any putative differences between the species investigated. For obviously the same amount of manure per square meter means a very different amount of nutriment for different plants; and, on the contrary, selection, however stringent it may be, is effective in analogously different degrees.

We conclude, therefore, that selection and nutrition influence the plant in the same direction and that it depends on circumstances whether the one or the other of the two preponderates.

Perhaps the simplest and clearest way of proving this generalization is to exhibit the means of the numbers of rays and ray-florets of the primary inflorescences of all the species investigated.

	1892	1893	1894	Increase 1893—1894
Anethum graveolens	18.3	21.2	25.2	+4.0
Chrysanthemum segetum	13—14	13.1	13.1	0.0
Coreopsis tinctoria	± 8	8.1	7.9	−0.2
Bidens grandiflora	± 5	5.2	4.9	−0.3
Coriandrum sativum	± 5	5.1	4.3	−0.8
Madia elegans	±21	18.9	17.9	−1.0

The varying result of the conflict between heavy manuring for three years and the selection of individuals with a small number of rays is shown by the figures in the last column.

I shall now exhibit the values for Q/M in a single table. Q, as we have already said, may be made independent of the nature of the varying character by dividing it by M; and in this way the amplitudes of variation of the different characters may be compared with one another. The subjoined values for Q/M are the means calculated from two or more generations in all the above cases. I have added *Oenothera Lamarckiana* to the list.

	$\frac{Q}{M}$
Anethum graveolens	0.16
Coriandrum sativum	0.11
Oenothera Lamarckiana	0.08
Bidens grandiflora	0.08
Madia elegans	0.08
Coreopsis tinctoria	0.04
Chrysanthemum segetum	0.03

The observed amplitudes of variation, estimated by this measure, differ considerably from one another. But they are, of course, also affected by selection and nutrition.

The phenomena of fluctuating variability are, there-

fore, caused by these two factors. The amount of hte deviation of any given character from its mean is determined partly by selection, i. e., by the characters of its parents and grandparents and partly by nutrition, i. e., by the operation of external influences on the individual itself. But the characters of the ancestors were also determined by the conditions of life; so we arrive at the conclusion that the phenomena of variability in the strict sense of the term, that is, the individual deviations from the mean of the species are solely caused by external conditions. Only it must be remembered that nutritional influences may be cumulative over several generations, inasmuch as only the best individuals will bear the best seed.

Fluctuating variability therefore falls within the province of the physiology of nutrition. The external causes of mutation are, on the other hand, as yet wholly unknown.

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MAN A CREATOR.

If man can truly be said to have been created in the image of God, he ought to evince his divinity by imitating the creator in deeds of creation, and this, indeed, has long been recognized as the worthiest occupation of man. The poet, the artist, the inventor, in fact all original thinkers and leaders, produce new forms, new devices and contrivances, new thoughts and higher ideals. Indeed it seems

as if the world were the mere raw material purposely left unfinished so as to enable man to exercise the divinest of his qualities, his creativeness. The imperfections of nature appear from this point of view as if made on purpose so as to offer man the opportunity of accomplishing this ambitious task and building up a human world above the natural. A late Latin proverb characterizes the pride of the inhabitants of the Netherlands in this line:

Deus creavit mare sed Batavus litora fecit.

"God created the ocean, but the shores have been made by Batavians."

The creativeness of man appears to acquire a special resemblance of God's own work, when it extends to the procreation of new species, and this has actually been accomplished of late by Dr. Nilsson, the Director of the Swedish Agricultural Station at Svalöf, and our reputed countryman Luther Burbank, of Santa Rosa, California. However meritorious these undertakings are, they remain exposed to the criticism of the narrow-minded, so we need not be surprised to find that Mr. Burbank was once called to account for arrogance by some ignorant clergyman who for the purpose of censuring him in the name of God, invited him one Sunday to his church, gave him a prominent seat in a pew exposed to the view of the congregation and denounced the supercilious ways of men who meddled with the plans of God by attempting to create new species. The incident is referred to by Mr. Harwood in his *New Creations in Plant Life,* (pp. 20-21) when he speaks of the troubles which Mr. Burbank encountered at the start of his career. He says:

"Opposition now came from many quarters. Not only did his friends see the fulfillment of their predictions,—some of them very kindly telling him so,—but people who had heard of some of the strange things he had done and who had not the breadth of vision to see what manner of man this was, pronounced him a charlatan,—a man who was creating all manner of unnatural forms of life, monstrosities, indeed a distinct foe to the race. A minister invited Mr. Burbank to listen to a sermon on his work, and when the guest was in the pew denounced him in bitter fashion as a man who was working in direct opposition to the will of God, in thus creating new forms of life which never should have been created, or if created, only by God himself."

The incident is comical enough, but it was not so humorous to Mr. Burbank at the time when his only consolation was the hope of proving to the world that his hopes were not the useless dreams of a visionary, but definite ideals the realization of which would raise mankind a step higher in civilization and actualize its divinity in a more complete sense.

Burbank's work stands now before the world and needs no further recommendation. He found out by experience, that to be a business man is one thing and to work for an ideal is another. He found that the business part had to be neglected for the sake of accomplishing the great task so near to his heart, and for this purpose Mr. Carnegie has come to his assistance by keeping a scientific station in Santa Rosa and aiding his work in general. Much has been written on Mr. Burbank, but mostly in a popular way by literary authors. Professor de Vries, however, has done justice to the significance of his labors from the scientific standpoint in his new book on *Plant Breeding*. P. C.

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